

The Growth, Production and Nutrition of

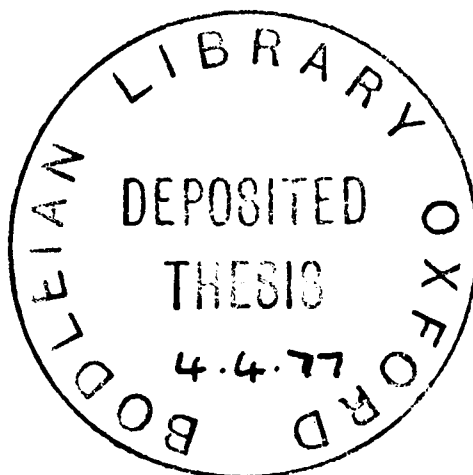
Rubus fruticosus L.agg. in Woodlands

**A thesis submitted for the degree of
Doctor of Philosophy in the University
of Oxford**

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To Philip



Theophrastus ca 300 B.C.

" Of the bramble again there are several kinds, showing very great variation; one is erect and tall, another runs along the ground and from the first bends downwards, and when it touches the earth it roots again."

ACKNOWLEDGEMENTS

During the three years of this project, I have received encouragement and useful advice from many members of the Departments of Agriculture, Botany and Forestry. I am deeply indebted to the late Dr. P.S. Lloyd for his supervision during the first two years and to Dr. H.C. Dawkins and Dr. S.R.J. Woodell for comments and criticisms during the third.

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Finally, my gratitude goes to Trudy Watt who for the last three years has put up with brambles everywhere.

ABSTRACT

This study examined patterns of growth shown by Rubus fruticosus L. agg. - the bramble-and looked at factors which controlled its growth. Literature on bramble ecology that was relevant to British conditions was reviewed. The study took place in Wytham Woods, a mixed, mainly deciduous wood. The soils varied from shallow limestone soils to heavy clays. Rubus vestitus Weihe and Nees was the most common bramble species.

Three sites were chosen ranging from one where bramble growth was very poor to one of the most productive bramble areas in Wytham. The changing distribution of dry weight within a bramble stand over a year was followed by splitting the plant into its components; leaves, laterals, canes of different ages.

The bramble stands were sampled on ten occasions during 1974 at four to six week intervals. All above ground material was removed from ten ^{one} metre-square plots from each area, at each sample time.

The overall pattern of dry weight change was the same for the three areas. Total biomass showed a summer peak, the result of three processes:-

- (1) The dry weight increase by first-year canes.
- (2) The initial increase and subsequent decline in weight of the second-year cane system because of growth and die-back of the laterals.

- (3) The final die-back of the cane system that had flowered the previous year. Standing dead, dead canes still attached to the rootstock and separate from the litter-layer - showed no seasonal change in dry-weight.

The dry weight increase by the laterals was of the same magnitude as that by canes. The main cane growth however was 5 - 6 weeks later than that of the laterals. Thus lateral leaves formed the bulk of the early summer canopy while cane leaves became more important in autumn and over winter.

Leaf area per plot was estimated from ^{direct} measurement of a sample ^{of known dry weight.} The winter bramble canopy was only half that in summer. Summer leaf-area-^{index} were 0.8 in the poorest bramble site measured, 2.1 in the best.

The main growth of canes and laterals was by increase in length. Total stem length per plot showed a summer peak.

Variations in both plant size and plant density (numbers/sq.m) caused the dry weight differences between the areas. Tree competition appeared to control these differences, the best growth occurring under an ash canopy, the worst under an oak/sycamore one.

Bramble biomass in Wytham was up to seven times greater than that reported for other sites in Britain. ^{Published values} Summer biomass of bramble in Britain range from 30-450 g/sq.m and annual turnover of dry weight from 50-300 g/sq.m/yr. This annual dry weight turnover is less than that for open-grown, herb communities, but similar to that for herb and shrub layers in British woodlands. Not all of this dry weight turnover represents current photosynthesis because there are transfers between roots, canes and laterals.

Over the year the bulk of the biomass was in the second-year

cane system. The turnover time for the standing dead was 1-2 years. Cycling of material in a bramble stand was thus faster than for woody shrubs.

A few rootstocks were excavated. The sizes of the root crowns matched the differences in shoot growth between areas. Crowns ranged from 5 - 60mm in diameter and ~~may~~ act as storage organs. The size and spread of the major roots, 4 - 6 per crown was also greatest in the areas of greatest shoot growth.

Records of flowering and fruiting were kept both per unit area and per cane. Flowering was less in areas of low vigour of growth, which were usually the most shaded. A direct correlation between length of laterals and flowering success was found by comparing flowering on regrowth canes, or defoliated canes, with the control canes for that area. Length of lateral and flowering success depended on the overall vigour of the cane and the laterals' position on it. Laterals on side branches and the terminal portions of canes were shorter and flowered less.

The process of tip-rooting was investigated. Root-boss formation increased when the tips of growing canes were covered by black fabric bags, but not when clear polythene bags were used. This confirmed the results of others that root-boss formation is increased if the stem apex is in the dark. Although defoliating canes reduced their growth it did not increase the number that tip-rooted.

The growth of the daughter plants was followed. The parent cane was cut at different times after the original tip-rooting and leaving different lengths of cane attached to the daughter plant. Transfer of material to the daughter plant was shown to start in autumn and continue until the following July. The material was largely derived from the metre of cane nearest to the daughter plant. Reverse

transfer, from daughter rootstock to parent cane can occur. Sections of parent cane separated from their parent root remained alive and bore laterals if attached to the daughter plant. Competition for cane reserves between laterals and daughter plants may occur, as in one experiment lateral growth was greater on canes separated from their daughter plants than where a daughter plant was present.

Tip-rooted canes were more abundant in areas of poor bramble growth than in vigorous areas. Such low vigour areas had a poorly developed stand structure such that cane tips were more likely to touch the ground.

Vegetative and floral reproduction were complementary within the areas considered. Flowering increased and tip-rooting decreased as the canes became more vigorous.

Non-destructive measurements were investigated as a means of recording bramble growth. Some measurements were made on individual stems, but the main emphasis was on plot-based measurements. These were calibrated against destructive sampling.

Point-quadrats were used for leaf-assessment. Changes in leaf-hits per plot agreed well with variations in measured leaf weight and area. Agreement was better for new leaves than for those which survived over winter, because the former were more horizontal.

Mean canopy height, derived from the heights of leaf hits rose in the summer during lateral growth and declined in autumn, partly because of lateral die-back from the tips, partly because of settling of canes under their own weight.

A dense bramble stand was found to have three layers; an upper leafy zone containing the bulk of the current canopy; a layer in which are the second-year canes and the remains of the previous years' canopy; the leafless lower layer containing most of the standing dead. Each year's canes grow through the lower layers and come to lie

horizontally as a result of their own weight and that of their laterals the subsequent year . In following years these canes are forced lower down the structure.

Intersection values were used to estimate stem quantities. These were a variant of Buffon's Needles technique, adapted by Newman (1966) for root length determinations. The number of stem intersections with rods placed across a plot was related to total stem length per plot. Stems differed greatly in angle which caused variation in the relationship particularly with the taller bramble stands.

Intersection values multiplied by height were well correlated with plot dry-weight, $r^2 = 0.8$. Regressions of dry weight on adjusted intersection values showed little difference for different times of the year.

These non-destructive methods were used to assess bramble stands which were too limited in area for repeated destructive sampling.

Part of the growth of first-year canes is based on rootstock reserves part on photosynthesis built up by the cane leaves. To separate these two, leaves on first-year canes were removed as they formed. This reduced cane growth by 20 - 50% relative to the controls. The reduction was greatest in areas of low vigour, which had the smallest rootstocks. The relatively small surface area of the canes made it unlikely that stem photosynthesis made a large contribution to growth of the defoliated canes. A large part of their growth was presumably therefore on rootstock reserves.

Autumn defoliation of first-year canes caused the same reduction of subsequent lateral growth as defoliation from the start of cane growth. This implied that the main build up of cane reserves was from September onwards. Defoliation of the laterals themselves

reduced lateral growth by about 50%, the least reduction being found on the thickest canes, which had the highest reserves.

Regrowth of bramble, after removal of top growth, was measured in two 100 sq.m areas. In first-year regrowth cane lengths were about 65% of those in the second-year regrowth which were equal to those in uncleared bramble. Lateral and leaf production in second-year regrowth were less than in the uncleared bramble, but by the third year the differences were very small.

Variations in bramble dry weight over the sampling areas were related to the presence of different tree species in the overstorey. Two surveys of the vegetation, by Field and Dawkins (In prepn.) and Lloyd (unpubl.), allowed further investigation of the relation between the nature of the overstorey and the bramble growth beneath it. Greatest growth in Wytham occurred under ash, least under sycamore or beech. Oak was intermediate. A shrub layer reduced bramble growth under an ash canopy, but had no effect on the amount of bramble under sycamore.

Non-destructive methods were used to compare growth of bramble under gaps with that in the surrounding shade. Under old gaps growth was 5-6 times that under the tree canopy. Gaps 7m across were created to determine the rate of response to a change in the overstorey. The dry-weight of bramble under the gaps, estimated by non-destructive methods, almost doubled in the year following the creation of the gap. A similarly large increase occurred in the next year.

concentrations.
The concentrations of magnesium, calcium, phosphorus, potassium and nitrogen were determined for leaf and stem material collected over the year. Potassium, magnesium and calcium were measured using a spectrophotometer after dry-ashing to remove organic material. Phosphorus was determined by the molybdo-vanadate yellow test. Nitrogen

was determined, after micro-kjeldahl digestion of samples, by the indophenol blue test.

Calcium concentrations were higher, potassium and nitrogen levels lower, in material from the most productive of the three bramble sites. This area had the highest soil pH and so probably also the greatest calcium availability. The lower potassium and nitrogen concentrations were probably caused by greater carbohydrate production "diluting" the minerals present. Absolute weights of all five elements in the bramble biomass were greatest in the most productive bramble area.

Falls in the concentrations of nitrogen, phosphorus and magnesium in the second-year canes, during lateral growth, indicated transfer of material to the laterals. The bulk of the mineral requirement for the laterals came however from fresh transfer to the second-year cane system from the roots. Total transfer of minerals from the roots to the second-year cane system was similar to that taken up by first-year canes, but about 60% of first-year uptake occurred after the maximum was reached in second-year canes. Total weight of minerals in the above-ground biomass reached a peak in the summer.

Falls in the mineral concentrations during die-back indicated that some minerals were withdrawn from stems and leaves prior to their death. The weight of minerals in the standing dead was small compared to the amount in the live shoots so that return of minerals to the rootstocks or to the litter must have been rapid.

The starch ^{concentration} of the dried stem material was determined by using the iodine-complex formation. Starch built up in first-year canes in the autumn after their ^{extension} had ended. There was a further rapid rise in starch content just prior to lateral growth beginning. This indicated that reserves were laid down in the autumn, but also that photosynthesis by the cane leaves in the spring was important. The

starch content of the canes fell during lateral growth.

A similar spring peak of starch content was found in the third-year canes and their laterals. This declined as die-back preceded, probably because of withdrawal of material to the rootstocks.

This study was the first to measure growth of bramble on ^{an example of} the productive sites found in many woods in Britain. The growth pattern found was similar to that for the less productive sites described elsewhere. The partitioning of resources within the plant was considered in various ways: first-year cane growth vs. lateral growth; transfer growth vs. current photosynthesis; floral vs. vegetative reproduction. Quantitative measurements were made of the bramble's response to tree competition particularly the nature of the tree canopy. From information on the internal and external factors which control growth an attempt was made to explain both the differences in growth between sites in Wytham and those between Wytham and other woods.

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INTRODUCTION

BRAMBLE ECOLOGY AND GROWTH

INTRODUCTION

1. The growth of Rubus fruticosus L.agg - the bramble or blackberry has received relatively little attention in Britain, despite its frequent occurrence in woodlands and hedgerows. Because it may suppress the growth of tree seedlings, bramble is a major obstacle to the simple regeneration of our hardwood forests. Bramble thickets hamper movement through woods and also invade grassland if the grazing pressure is reduced.

2. In this study I examined the pattern of bramble growth found in Wytham woods and some of the factors which operate on the plant to determine this pattern. Various aspects of bramble growth were examined: phenology, reproduction, internal changes, annual turnover of dry weight. Comparisons were made between growth in Wytham and at other sites.

SOME ASPECTS OF BRAMBLE ECOLOGY

3. **BRAMBLE IN GRASSLAND** During the change from grassland to scrub dense thickets of bramble frequently occur. On some sites it is a pioneer, (Adamson 1932) and other species establish within the protection of its thickets. These areas of bramble and associated

species spread and coalesce. The trees and shrubs assume dominance and may eliminate the bramble. Often, however, the bramble persists into the woodland phase.

4. On shallower, limestone soils, Watt (1934) found bramble to be less competitive with grassland. It was unable to assume or maintain dominance in the open and was abundant only where some overhead canopy had developed. Where it did occur on the commons it was less vigorous than under woodland.

5. The invasion of grassland from nearby thickets or hedgerows is usually by bramble stems that root at their tips. Daughter plants formed in this way have a larger food base than seedlings. They are thus better able to establish in a closed, highly competitive community.

6. **BRAMBLE IN WOODLAND** In mature woodland bramble may form the shrub layer giving a continuous canopy which may be over one metre high. The herb layer associated with a dense stand of bramble is generally poor. Sometimes a joint Pteridium-Rubus society is formed (Tansley 1949). Watson (1958), however, considered that bramble tended to die out where bracken was dominant. This may be because, on bracken-dominated sites, fire or grazing is present which controls the bramble.

7. **SHADE TOLERANCE** Salisbury (1918) showed that bramble can tolerate low light levels during the growing season and survive for several years under deep shade, though often as stunted individuals. If conditions change, as when a coppice cut is taken, there is an increase in the growth of those plants already present and an invasion

of bramble seedlings. Most of these latter die out as regrowth of the trees takes place and the overhead canopy is restored.

8. For beech Watt (1934) found that the height and density of the bramble below varied with the degree of cover. Bramble was eliminated under the deep shade of young beech, but often reappeared in the older stands. Kerner (in Conard 1951) reported that death of the bramble layer during the early growth of a pine stand was quicker than under beech. The presence of a shrub layer may lead to bramble dying out even under a species, such as ash, which has a diffuse canopy (Watt 1924). The species comprising the bramble aggregate differ in their tolerance to shade.

9. SOIL REQUIREMENTS In the oak woods of Hertfordshire, Salisbury (1918) found bramble on a wide range of soil conditions. In beech woods (Tansley 1949) Rubus appears to be associated with the brown earths, rather than the podsoils or rendzinas. Very wet soils are avoided. (Beijerinck 1953). R. ~~trivialis~~ is more tolerant of wet, clay conditions than most species in the bramble aggregate, while other species, such as R. vestitus, are more commonly found on limestone soils. (Watson 1958).

10. DISTRIBUTION DIFFERENCES BETWEEN SPECIES In Sweden Orredson (1975) found a correlation between the distribution of five groups of bramble species and winter conditions. These groups were distinguished by the time of autumn leaf-fall and the onset of dormancy.

11. In Holland Beijerinck (1952) found that species in relict woodlands were different from those found in more modern woods. Species

normally found near roadsides or in open spaces formed a third group. Some species, including R. vestitus, were too infrequently met with to classify in this way.

12. The longer a site remains free from disturbances the more bramble species it is likely to contain (Allen D. 1971). In managed woods there are periodic changes in conditions as a result of tree growth and forestry operations. The bramble population is thus frequently subject to fluctuations. Such woods are likely to contain only those species common in the area as a whole.

13. **GRAZING SUSCEPTIBILITY** Closely grazed pastures are not normally invaded by bramble. Grazing and trampling prevents the establishment of either daughter plants or seedlings. Because of their armature older leaves and stems are not normally eaten by rabbits (Tansley 1949), cattle or sheep (Amor 1971). In a bramble thicket the older growth may protect the younger from grazing. Goats have been used to control bramble bushes in New Zealand (Von Pein 1961).

14. Fallow deer in Wytham were seen to eat the leaves in winter when little else was available. In the New Forest Jackson (in Chapman 1975) showed that deer ate bramble leaves all-year-round, but particularly in winter, when up to 20% of their diet was bramble.

15. **BRAMBLE AS A WEED** In Britain bramble is a weed mainly in lowland hardwood forests. Regeneration is suppressed and movement through stands hindered. Control measures are described by Brown (1975). In other areas of the world bramble is far more serious as a weed of pasture. Amor (1971) and Northcroft (1927) describe the problems with

PARTS OF A BRAMBLE PLANT

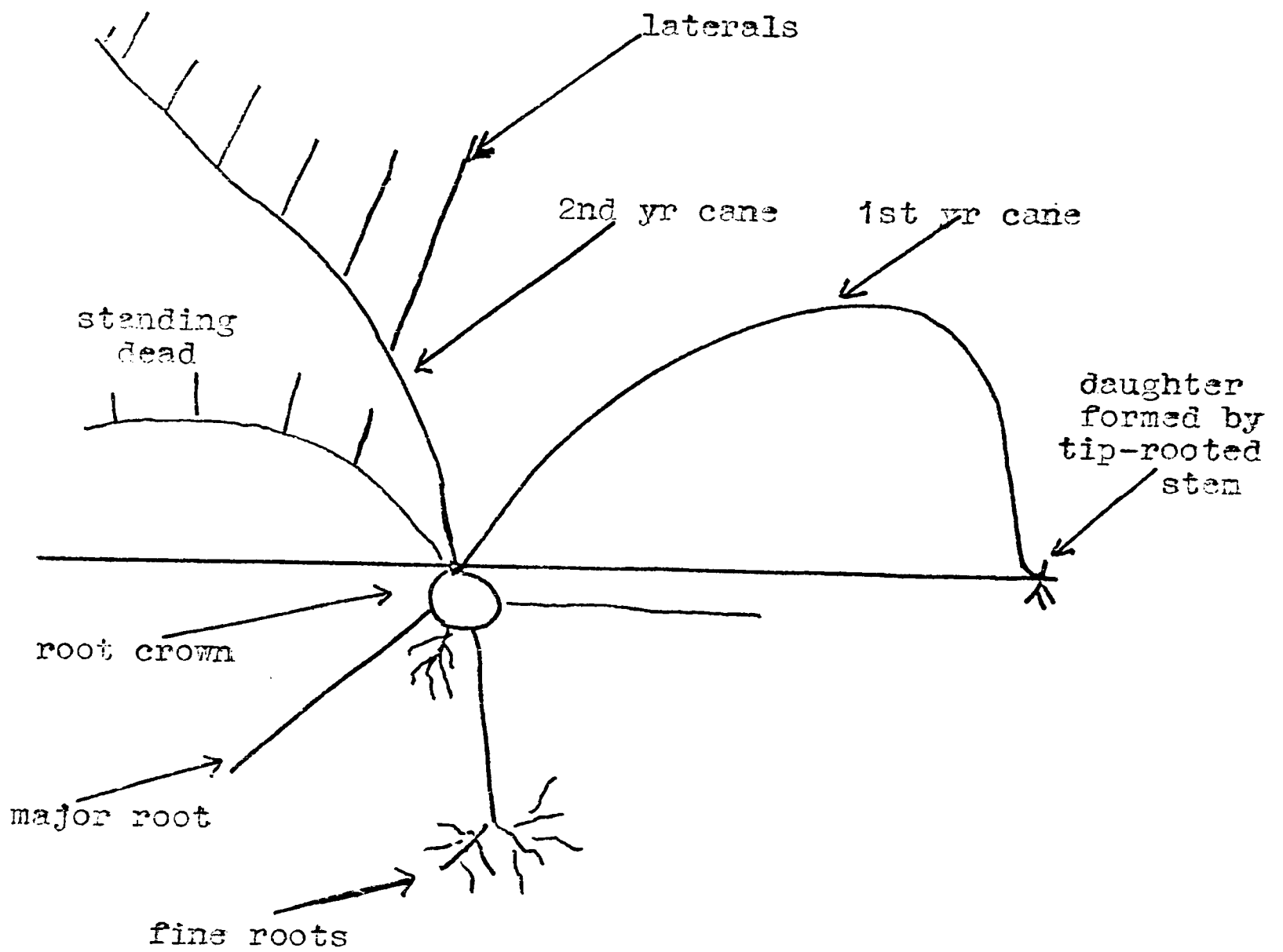


Table 1

TABLE 1

	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
1st yr. canes			Canes emerge from ground	-----		Growth ends	Some canes tip-root					
						Cane leaves reach maximum						
2nd yr. canes + laterals			Cane leaves lost	-----								
			Lateral growth begins	-----	Flowering & Fruiting			Die-back	-----			
					Lateral leaves reach maximum							
3rd yr. canes + laterals			Die back of most canes continues	-----								
			Some produce further laterals		"Tertiary" growth.							

APPROXIMATE TIMING OF EVENTS IN THE LIFE OF A BRAMBLE CANE

introduced bramble species in Australia and New Zealand respectively.

GROWTH AND DEVELOPMENT OF BRAMBLE

16. Growth of an individual bramble cane is described in detail by Heslop-Harrison (1959). The main features are considered below with reference to growth in Wytham. Figure ^{P.1} 1 illustrates the different parts of the bramble plant, while Table 1 provides a rough calendar of events, based on observations in Wytham during 1974.

17. **FIRST-YEAR CANES** First-year canes develop from buds on the root crown. Most crowns produce at least one cane each year. Initially the cane grows vertically, but later in the summer it bends over. Extension ends in the autumn with a series of shortened internodes, or further growth, downwards, may result in the stem rooting at its tip. From this a new plant is formed. Canes in Wytham range from about 50-400 cm long. Northcroft (1927) reported canes 600cm long in New Zealand.

18. **LATERAL GROWTH** In its second year buds on the cane grow out to form the laterals. These grow nearly vertically and usually end in an inflorescence. The leaves on the cane are lost, but new leaves are borne on the laterals. If the cane tip is damaged while it is growing, laterals may be formed in the first-year. These, however, do not flower but themselves bear laterals, that do flower, the following year.

19. **DIE BACK** Canes and laterals start to die back in the autumn, after fruiting. Death of the whole cane is usually complete by the following summer. Most canes are thus biennial.

20 "TERTIARY" GROWTH Laterals formed in the second year sometimes remain vegetative. These do not die-back in the autumn. They behave as first-year canes and bear flowering laterals the following year. These were rare in Wytham.

21 More common was the production of fresh laterals on laterals that had themselves flowered the previous year, or directly on three-year old canes. Such "tertiary" laterals were usually thinner and shorter than normal. The numbers of such laterals in a bramble stand were small compared to those borne on second-year canes.

22 **STANDING DEAD** After a cane has died it may remain attached to the rootstock, and distinct from the litter layer, for 1 - 2 years. Such dead canes are held up by the live stems with which they are interlaced. These dead canes and laterals form the category subsequently referred to as "standing dead."

23 **ROOTSTOCKS** The rootstocks of bramble are perennial. Amor
 crowns
(1971) found ~~some~~ up to eight years old. The root system consists of
a central crown - up to 6 cm across in Wytham - major roots and the
fine rootlets. The major roots were found to spread to nearly a metre
from the largest rootstocks in Wytham. Northcroft (1927) reported spread
of up to 8m. The bulk of the roots were found by Amor (1971) to be
within the top 20 cm of soil.

INVESTIGATION OF BRAMBLE GROWTH

IN WYTHAM

SCOPE OF THE STUDY

24 SEASONAL GROWTH CHANGES Bramble was sampled by periodic

TABLE 2

HIGH, INTERMEDIATE AND LOW BRAMBLE
AREAS IN WYTHAM.

Table 2

	Area A	B	C	
Summer biomass	438	277	149	g/sq.m
Bramble canopy height	75	45	30	cm from ground.

harvests at three sites in Wytham. At each site bramble was the most obvious component of the ground flora. The amount of bramble present, however, differed greatly between the three sites. ^{p. 9} Table 2. The timing, amount and distribution of growth at the three sites were measured and compared.

25 MINERAL AND STARCH CONTENTS Material from the above sampling programme was analysed for ^{concentrations} of magnesium, calcium, phosphorus, nitrogen and potassium. The stems were also analysed for their starch ^{concentrations}. Changes in the concentrations and total amounts of these nutrients in leaf and stem were related to growth changes.

26 MEASUREMENTS ON INDIVIDUAL STEMS The growth of individual canes and laterals was measured. The occurrence of tip-rooting by canes, and flowering on laterals was noted. The effect of defoliation on stem growth was investigated.

27 NON-DESTRUCTIVE SAMPLING The relations between destructive and certain non-destructive forms of sampling were determined. This allowed a wider range of bramble stands to be investigated than was possible by periodic harvesting.

28 OVERSTOREY AND BRAMBLE GROWTH Two surveys of parts of Wytham Wood, by Field and Dawkins (In prepn.) and Lloyd (unpublished) enabled the growth of bramble under different tree canopies to be compared. The response of bramble to the creation of small gaps in the canopy was measured.

THE FIELD AREA

29 DESCRIPTION OF THE WOOD The work was carried out largely in

Wytham Woods, a few miles north-east of Oxford, between 1973 and 1976. Grayson and Jones (1956) deal with the history of the wood and its management prior to this century. After 1900 some areas were replanted, partly with conifers most of which have since been removed. The wood is predominantly oak, ash, sycamore and beech. A substantial area of the woods are planted, the rest is irregular and uneven-aged.

30 SOILS The surface geology is very varied. At the top of Wytham hill are shallow soils over Coral Rag limestone. Lower down are sandy soils derived from Calcareous Grit, while towards the bottom of the hill the soils are on Oxford Clay. In many places round the hill large blocks of limestone have "slipped" down the slope and are now found well below the level of the original Coral Rag.

31 THE WYTHAM GRID During 1973 and 1974 a grid, based on the Ordnance Survey National Grid, was laid out in the woods by Field and Dawkins. Posts were placed at 100 m intersections. The areas in which the work was done could thus be located by reference to the nearest grid post(^{P. 12} Table 3).

BRAMBLE SPECIES PRESENT IN STUDY AREAS

32 COLLECTION AND IDENTIFICATION OF SPECIMENS For identification purposes a bramble specimen should contain a section from a well-grown, vigorous, first-year cane as well as examples of flowers and young fruit from the same plant. The plant should be growing in the sunlight (Watson 1958). Full development of the characteristic stem armature may not be shown by young or weak canes, or those growing in the shade.

33. When the areas were selected, in which the work was carried out, it was not possible to be certain that the species were the same in each. All the plants were growing in some form of shade. Also the choice was made in winter when only vegetative characteristics were visible.

34. In summer 1974 representative samples were collected from the areas of the obvious varieties of bramble present. These were kindly identified for me by A. Newton, 11 Kensington Gardens, Hale, Cheshire. The specimens are now stored in the Fielding. Druce Herbarium, Botany School, Oxford. In each area Rubus vestitus Weihe and Nees was the main species^{P.12} (Table 3). R. dasyphyllus. Rogers. was also found in some of the areas and R. raduloides. Sudre. in other.

35. Watson (1958) classes vestitus and dasyphyllus as common in southern Britain, raduloides as rather infrequent except in the west. All had been previously recorded for Oxfordshire and Berkshire. R. vestitus is considered more tolerant of clay and limestone soils than some members of the bramble aggregate, which may explain the abundance of this species in Wytham.

36. Because mixtures of bramble species were present in most of the areas, the aggregate name is used in most of this thesis. Bramble and blackberry are used interchangeably as the English equivalents of Rubus fruticosus L.agg. Names of species other than bramble follow Clapham, Tutin and Warburg (1962).

37. EFFECT OF SPECIES MIXTURES ON COMPARISONS BETWEEN AREAS Bramble species within the aggregate differ in their growth rate, habit and

environmental tolerances. Most bramble stands contain two or more species. When comparisons are made between areas therefore, treatment or environmental differences between the areas may be confounded with variations in species composition. When comparisons are made within an area, there is a greater chance that all the canes measured belong to the same species, because of the importance of vegetative spread in thicket formation.

38. The same problem arises when comparisons are made with results from other workers, particularly as the species present are seldom identified. Despite this, however, it was thought that a useful general picture of bramble growth under field conditions could be built up from the Wytham results.

DRY WEIGHT CHANGES IN A BRAMBLE STAND OVER A YEAR

METHODS AND MATERIALS

SITES

39 Periodic sampling of bramble dry-weight was carried out in areas A, B, C during 1974. A had the largest standing crop of bramble, C the smallest. There were no signs of recent disturbance of the sites, so it was assumed that the bramble growth at each was reasonably in equilibrium with its environment. ^{P.12} Table 3 summarises site details.

40 TREE COVER All three areas were plantations. These provide more uniform tree cover condition than found in other parts of the wood. The tree canopy in B was entirely oak, A mainly ash, but with a few scattered oaks. C was mixed, but largely oak and sycamore coppice-regrowth. There were scattered hazel bushes in all three areas, but these were insufficient to form a distinct understorey. One "block" in B was resited because it fell within an area of very dense hazel. The bramble in this part of the stand was markedly different from the rest.

41 SOIL Soil samples taken by auger revealed no discontinuities in soil type within each area. Soils in B and C were similar, both sandy loams derived from Calcareous Grit. The soil in A was heavier and probably formed from Oxford Clay. Fragments of limestone were present in the soil in A, derived from a nearby block of Coral Rag that had "slipped" down the hill. As a result the soil pH was

greater in A than in B or C (^{P. 12} Table 4).

42 GROUND VEGETATION The sites were chosen for the relative uniformity of the bramble cover within them. Some parts of C were, nevertheless, virtually bare of bramble. In A and B cover was nearly continuous, but the height and vigour of the bramble growth varied over the areas.

43 In each area bramble was the species making the greatest contribution to the ground-flora biomass over the year. In B and C the other species present were mainly small herbs: Mecurialis perennis, Endymion non-scriptus, Circaea lutetiana. In A tall herbs and grasses predominated among the non-bramble species: Carex pendula, Deschampsia caespitosa, Urtica dioica.

SAMPLING PROCEDURES

44 ROOT SAMPLING In a plant such as bramble, with short-lived shoots and perennial rootstocks, a large amount of material may be exchanged between roots and shoots. However, there was no quantitative sampling of the root system for the following reasons: the range of sizes shown by the crowns and the major roots; the spread of the major roots; the problems of root identification. The results of partial excavation of a number of rootstocks are described on page 71.

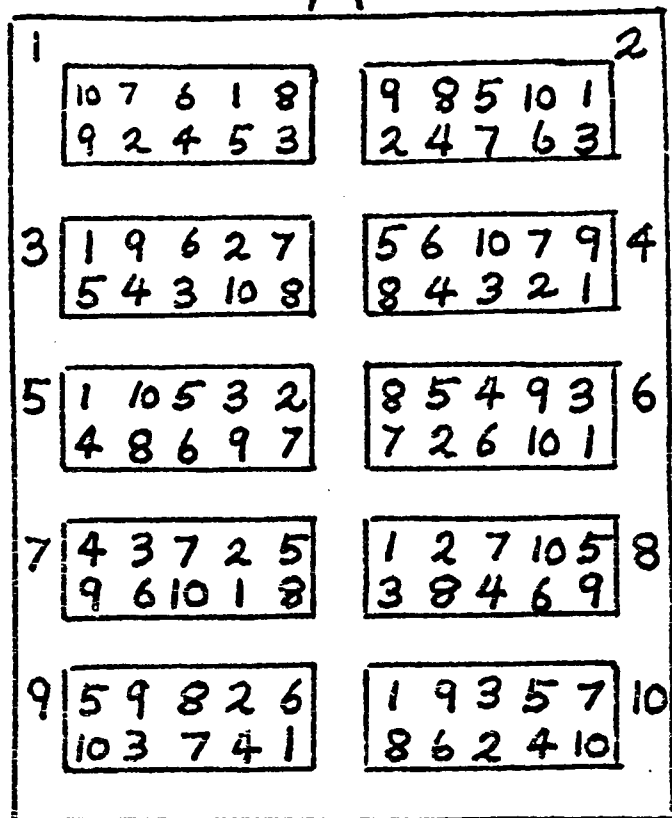
45 WHOLE-CANE SAMPLING vs AREA BASED SAMPLING Sykes and Taylor (In press), in a study similar to this, used a circular plot as the sampling unit. The circle was defined by a central peg and attached chain equal to the circle radius. All canes rooted in the circle were removed including those sections of the canes that were outside the circle itself. Information about individual canes

was thus collected at the same time as information on biomass per unit area. This method would have been difficult to apply to the areas sampled in this study because of the length of the canes and their mutual entanglement. The area around each plot disturbed by this type of sampling would have been large and difficult to define.

46 In this study all bramble material within the plots was removed, whether rooted in the plot or not. Information about particular canes was lost, but the boundaries of the plot were known. It was thus easier to move through the stand without disturbing plots yet to be sampled. Sections of canes outside the plots that were severed from their rootstock, by the sampling, died. The general canopy structure, however, was not greatly affected by the sampling.

47 A distance of two metres between neighbouring plots was found to be the minimum necessary. With this distance the maximum stem length in one plot that was affected by the cut boundary of another was found to be 0.24% of the total stem length in that plot. During the sampling period no evidence was seen of one plot's sampling affecting the bramble in another.

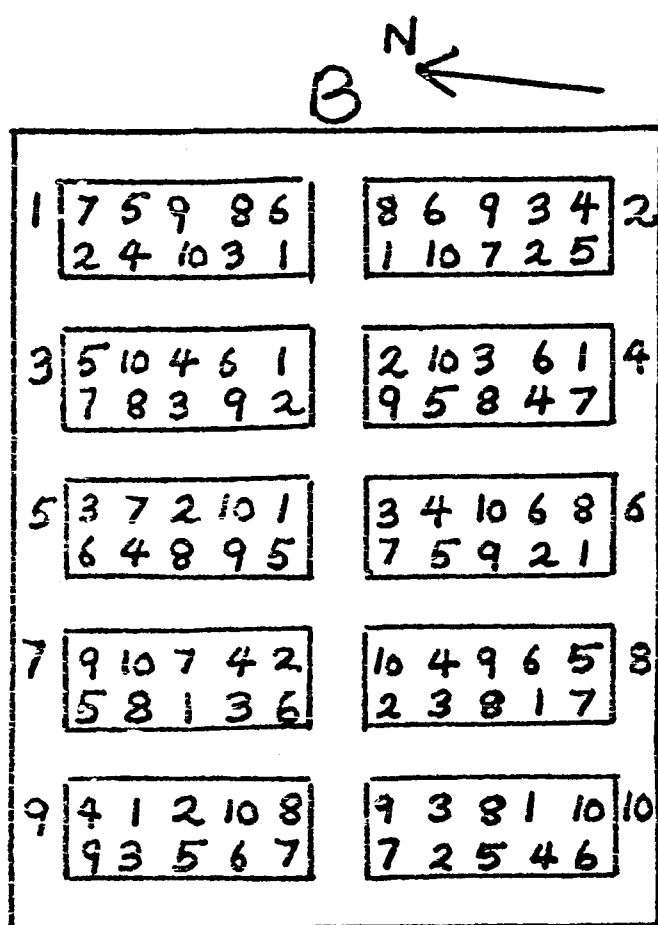
48 SIZE AND SHAPE OF PLOTS Errors arose in determining the exact point at which a stem crossed the edge of a plot. Removing one cane often caused movement of others such that their position relative to the edge was altered. Circular plots had the lowest edge-to-area ratio. They were, however, more difficult to lay-out than square plots and following the edge of the latter was easier. Square plots were therefore used. Edge errors were greatest in A which had the most stems per unit area and was the tallest of the bramble stands.



ARRANGEMENT OF PLOTS

Nos within blocks indicate the harvest to which each plot was assigned.

5mm = 3m



Individual plots.

10mm = 1m

Shaded area harvested

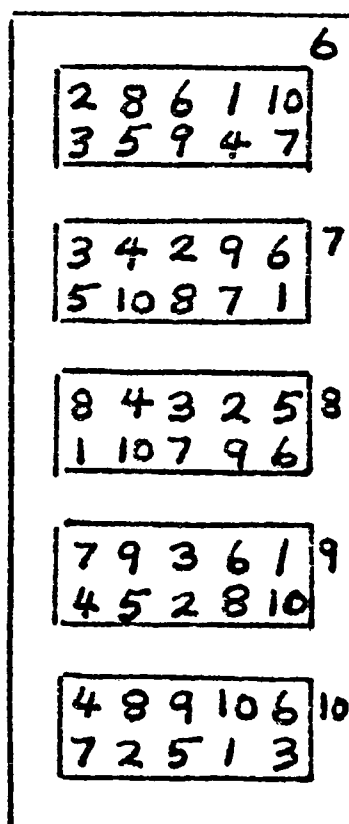
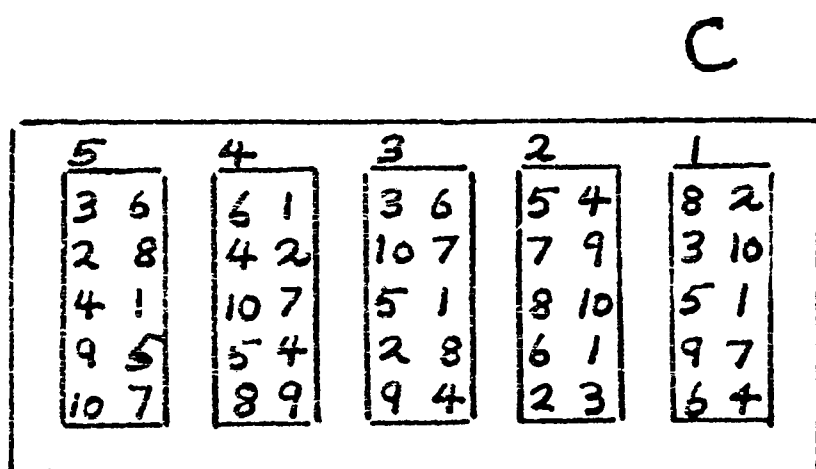
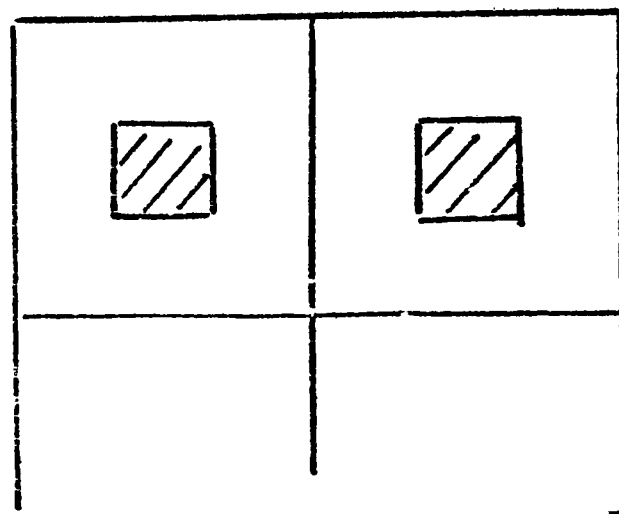


TABLE 5

TIMES OF HARVESTS

Table 5

Harvest no.	Dates	Order of harvesting
1	10-22 Jan. 1974	C B A
2	21-28 Feb. "	C B A
3	28 Mar.-2 April "	B C A
4	3-9 May "	B C A
5	4-11 June "	A B C
6	4-10 July "	B C A
7	14-19 Aug. "	B C A
8	17-23 Sept "	C B A
9	29 Oct.-1 Nov. "'	B C A
10	15-17 Jan. "	A C B

49 One metre-square was chosen as being the most convenient size of plot for use in both the smallest and largest bramble stands in Wytham. With smaller plots the number which failed to contain a rootstock greatly increased, increasing the between-plot variability.

50 TREES IN SAMPLE PLOTS Small trees occurred frequently in the sample plots, i.e. trees occupying less than 5% of plot area. No correction was made for these. In a few plots in A and C (less than ten each) more than a quarter of the plot was occupied by a tree. In such cases the plot was "moved" by the minimum amount needed to exclude the tree, to reduce between-plot variation. This introduced an error into any calculations of total bramble for the whole stand, as the area occupied by trees was underestimated. This error was about 5% or less and so small compared to other field errors.

51 LAY-OUT OF PLOTS In each area one hundred plots were marked out in ten blocks of ten (^{P.18} Fig.2). A 3m gap between blocks allowed any plot to be reached without disturbing the rest. Before sampling started each plot was assigned at random to one of the ten harvests, one plot from each block to every harvest.

52 TIMING OF HARVESTS Sampling started in January 1974 and the last harvest was in January 1975. The order of sampling the areas varied, but there was normally only a few days between them (^{P.19} Table 5)

53 HARVEST PROCEDURE Each metre-square to be sampled was marked out with four bamboo rods laid along the ground with four others to mark the corners. Before any of the plots in an area were cut, they were assessed using non-destructive methods which

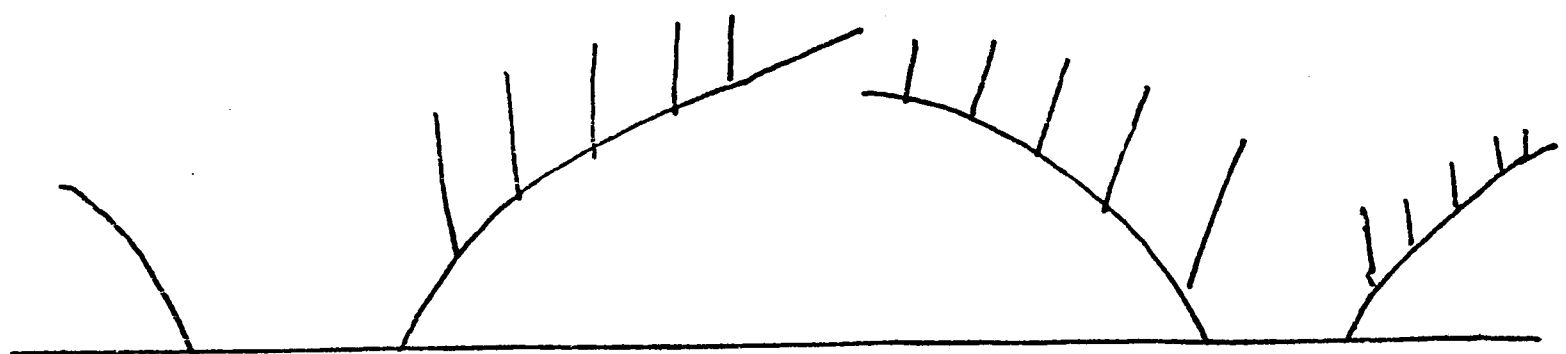
are described on pages 102 - 144. All bramble material within the plot, including standing dead, but excluding litter, was then removed and tied in a bundle. Canes and laterals were measured as they were cut to obtain total-stem-length per plot. The number of canes per rootstock and the position of each rootstock in each plot were then noted.

54 The bundles from each area were taken to the University Field Station, Wytham, for sorting and drying. No estimate is available of losses from the bundles during transport. Such losses were probably small as the spines tended to hold leaves and stems together. The dead, brittle stems which might have been lost were placed in the centre of each bundle.

55 SORTING AND DRYING At the Field Station each bundle was sorted into its components: leaves, stems of different ages, standing dead. These were dried at 105°C before weighing. Leaves were weighed after overnight drying, stems were left longer, although Allen (1974) found that there may be losses in dry-weight with drying periods greater than 24 hours at this temperature. The time between a plot being harvested and entering the oven varied with the area and number of plots harvested in a day. It was usually less than six hours. Quantities greater than 5g dry-weight were weighed to 0.5g, smaller quantities to 0.1g. Field errors were such that there was no justification for greater precision in the weighing.

56 MEASUREMENT OF LEAF AREA For harvests 1 to 8 a sample of fresh leaves was kept separate. The leaf area of these samples was then measured on a machine built by Dr. Martin, Department of Agricultural Science, Oxford. An estimate of specific leaf area and total leaf area per plot could thus be obtained. There was not

CANE SYSTEMS & COMPONENTS PRESENT IN EARLY SUMMER 1974



1st yr, canes beginning to grow	2nd yr. cane system with laterals about half-grown	3rd yr cane system canes and laterals dying back.	Standing dead
74 canes	73 canes	72 canes	
74 cane leaves	Remains of 73 cane leaves		
	74 laterals	73 laterals	
	74 lateral leaves	Remains of 73 lateral leaves	

enough time for this to be done at harvests 9 and 10. These samples for area determination were the only material to be kept overnight before they could be dried. Polythene bags containing the samples were put into refridgerators.

57 **LENGTH GROWTH OF CANES AND LATERALS** The lengths of individual canes and laterals were measured during the growing season. Five representative rootstocks were selected in each area in March 1974. On each rootstock the growth of an emerging first-year cane was followed and also, the development of laterals on a second-year cane. Measurements were made at monthly intervals during the season until growth ended.

RESULTS *

58 **NAMING OF PARTS** Stem and leaf material of several ages was present during the sampling period. To distinguish these each component was given a prefix to indicate the year in which it developed. Leaves formed in 1974 were separated into those borne on canes and those borne on laterals, though this was not done for the leaves which survived from 1973.

59 **CANE SYSTEMS PRESENT** During late spring and early summer three distinct cane systems were present: the developing first-year canes; second-year canes bearing developing laterals; third-year canes, the remains of the system which had flowered the previous summer. In addition there was the standing dead. These different types of cane are shown diagrammatically in Fig. 3. ^{P.22} The changes in dry-weight for each are shown in Fig. 4. ^{P.24, 25.}

FIRST-YEAR CANE SYSTEM

60 **74 CANES AND CANE LEAVES** 74 canes emerged from the litter layer towards the end of April. Growth probably started about a

* For details of the statistical method used to determine the significance of dry weight changes in each component over the season see APPENDIX 2.

DISTRIBUTION OF DRY WEIGHT BETWEEN COMPONENTS OVER THE SEASON

350 g/sq.m

g/sq.m

1st yr. canes

2nd yr. cane system

3rd yr. cane system

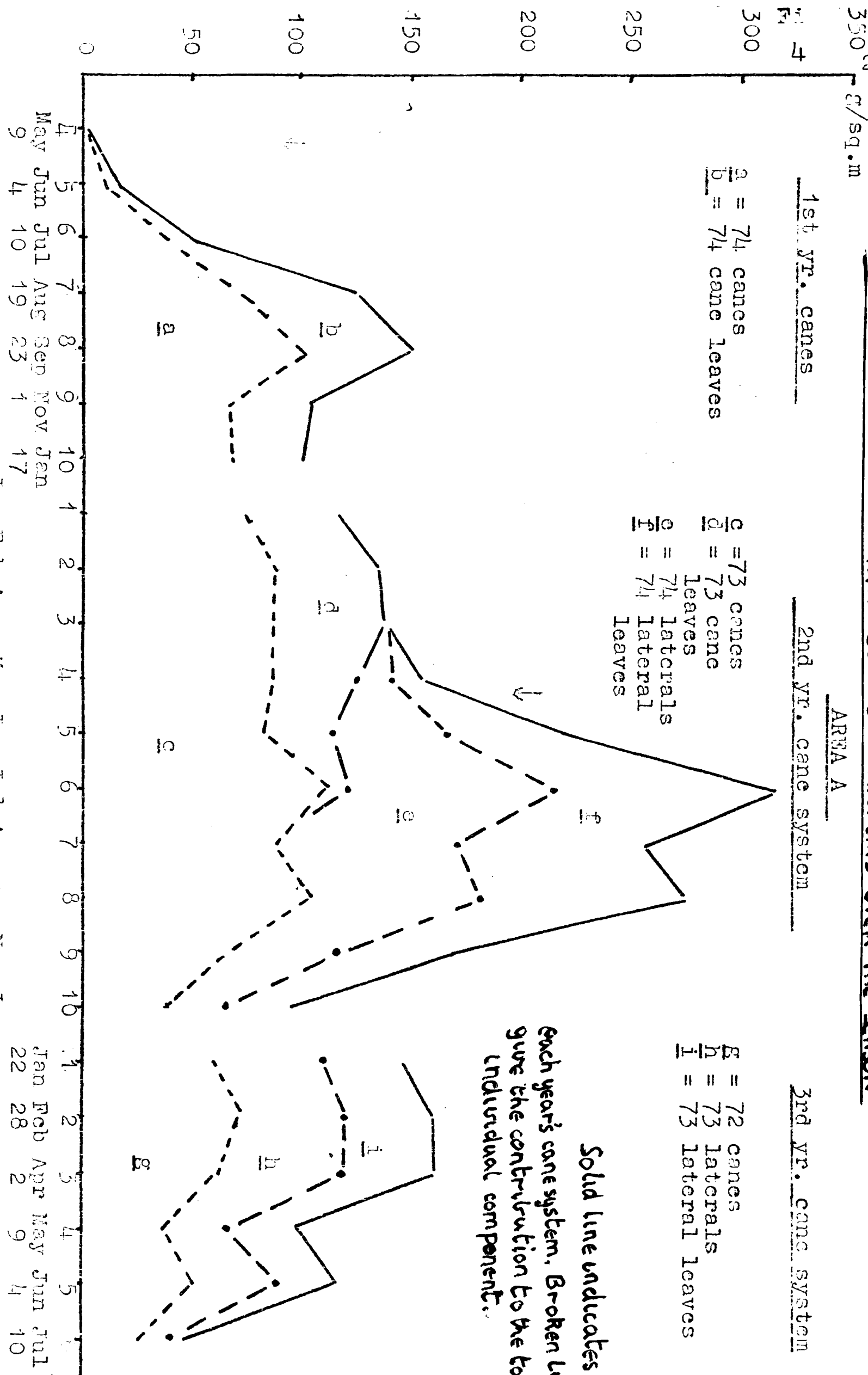
AREA A

a = 74 canes
b = 74 cane leaves

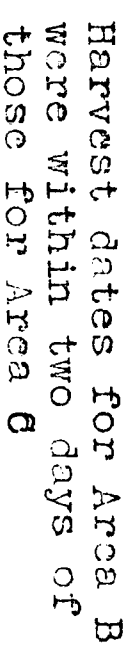
c = 73 canes
d = 73 cane leaves
e = 74 lateral leaves
f = 74 lateral leaves

g = 72 canes
h = 73 lateral leaves
i = 73 lateral leaves

Solid line indicates total weight of each year's cane system. Broken lines and letters give the contribution to the total by each individual component.



HARVEST NO.



month before this. There was then a period of rapid increase in dry-weight of leaf and stem which ended about mid-August. There was no change in weight over autumn and winter. Some of the lowest leaves were, however, lost during the growing season.

61 SAMPLING ERRORS The peak at harvest 8 in area A was not statistically significant. The more gradual increase in dry-weight shown in area C was more likely a result of greater sampling errors, relative to the final weight of cane per unit area, than of a different pattern of growth to A or B.

SECOND-YEAR CANE SYSTEM

62 73 CANE LEAVES 73 leaves were not separated into those borne on laterals and those borne on canes. The quantities of 73 cane and lateral leaves in Fig.4 are thus based on the relative proportions of each type of leaf found at harvest 10. The old cane leaves had disappeared by August. Some were shaded out by the new bramble canopy formed above them. Others may have been forced off by growth of the laterals, particularly where two laterals formed at a node. It was not known how much of the loss in weight of 73 leaves per unit area over the early summer was a result of withdrawal from the leaves, and how much caused by loss of entire leaves.

63 73 CANES Sykes and Taylor (In press.) report a decrease in dry weight of the cane during growth of the laterals, which suggests a transfer of material to the laterals. Only B showed such a drop over the period of lateral growth. Any material withdrawn from the cane leaves may also be available for lateral growth. From the dry-weight data alone, however, there is little evidence of the importance of transfers in lateral growth by bramble in Wytham.

TABLE 6

FLOWERING AND FRUITING

Table 6

	Area	A	B	C	
Inflorescence no./sq.m		20.9 ±1.5	11.5 ±1.3	5.0 ±1.5	mean of 10 plots
Infl. no.		0.25	0.28	0.28	
<u>Lateral dry wt.</u>					
Infl. no. fruiting		13.4 ±1.9	2.2 ±0.5	0.1 ±0.1	"
% failing to fruit.		36	81	98	

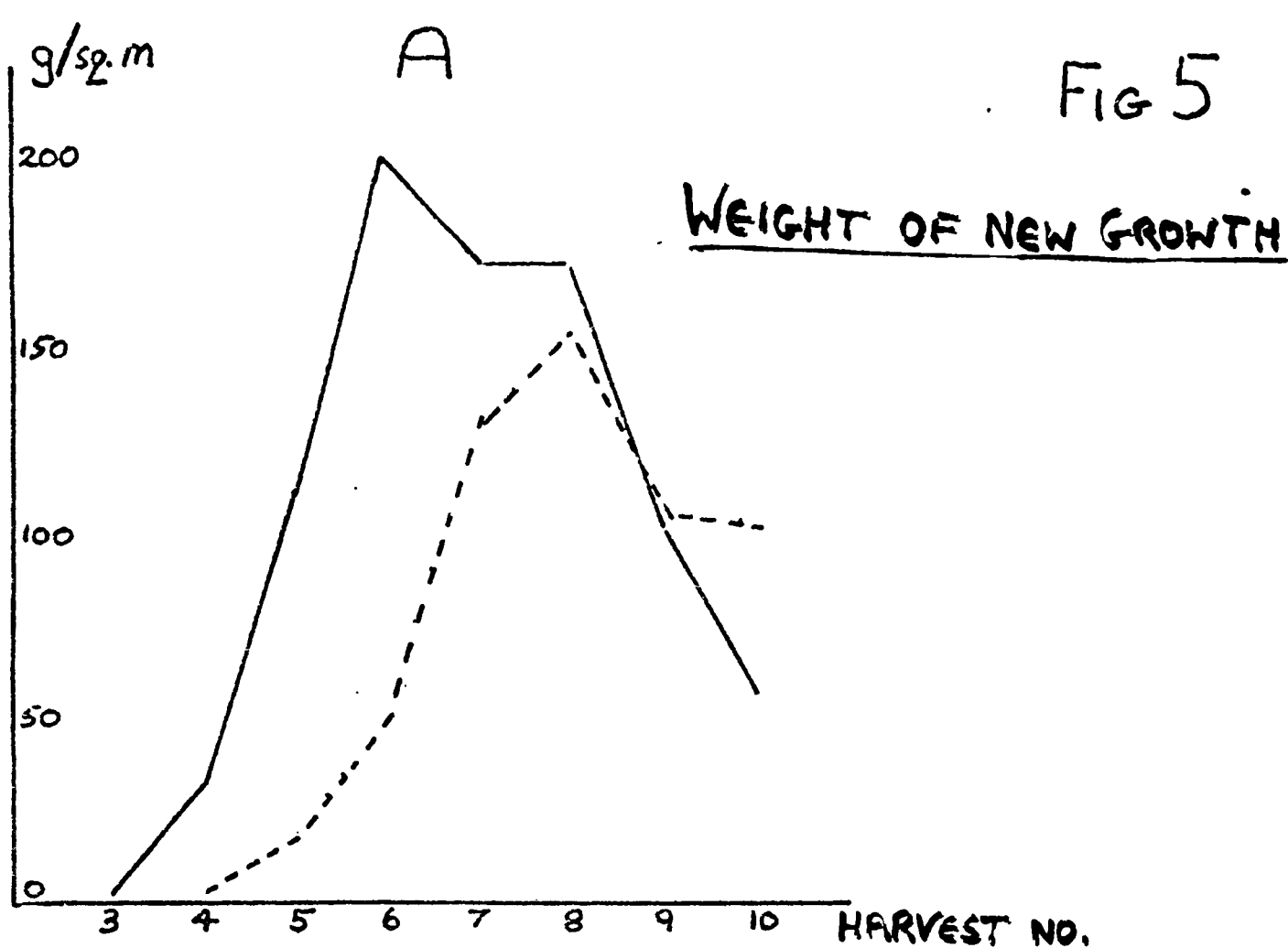
64 GROWTH OF 74 LATERALS The buds started opening towards the end of March. Increase in dry-weight ended in June-July with the formation of inflorescences. Lateral leaf weight reached a peak at the same time.

65 FLOWERING AND FRUITING Flowering and fruiting were most abundant in area A (Table 6)^{P.27}. The number of inflorescences relative to the weight of laterals per plot was similar for all three areas, but inflorescences in A were bigger. The fruiting success for inflorescences declined from A to C. In this study, however, it was not possible to say whether the better flower and fruit production in A was a direct result of the greater growth in A or whether some external factor such as light increased growth and flowering simultaneously, but independently. The two possibilities are inevitably confounded.

66 AUTUMN DIE-BACK OF SECOND-YEAR CANES Die-back of the stems started in the autumn after flowering and fruiting. In C the loss in stem weight over the autumn was not significant although lateral-leaf weight declined sharply. A and B, however, both showed sharp falls in lateral, leaf and cane weights from H8-10 and H7-10 respectively. Some withdrawal of material prior to death probably occurred, but the main loss in dry-weight appeared to be the result of death of sections of canes or laterals.

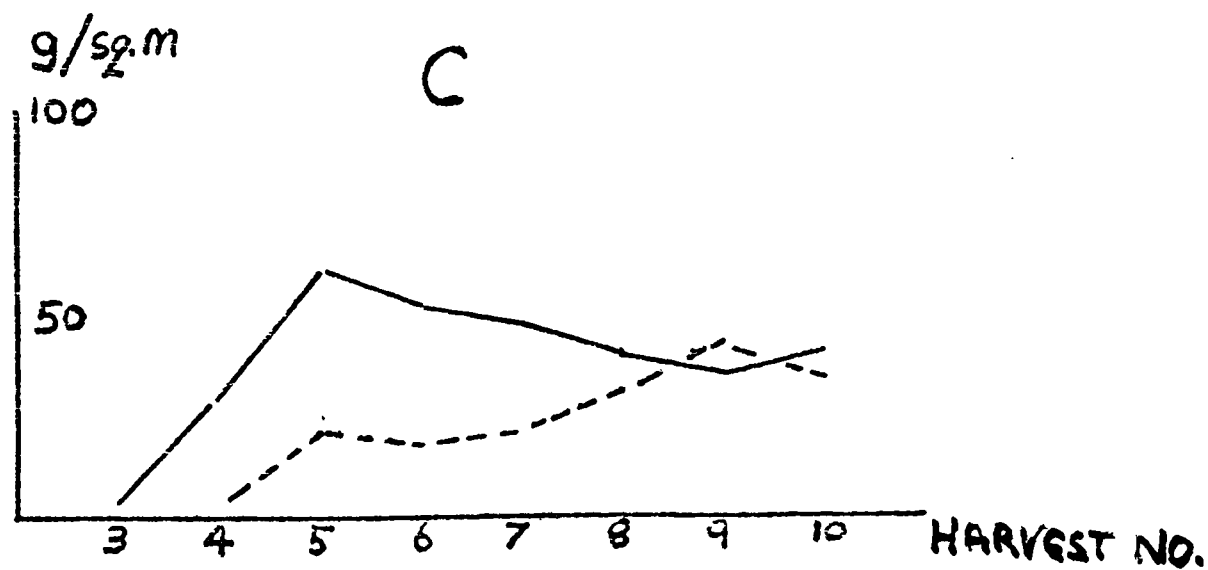
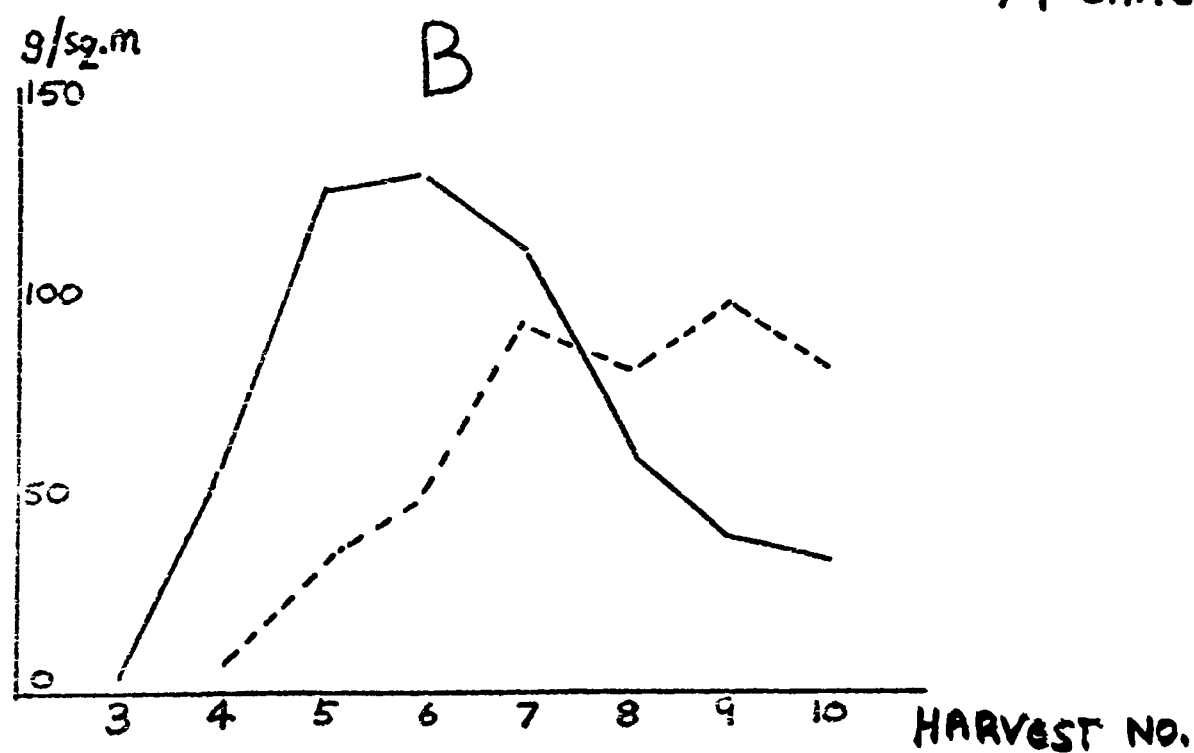
67 VARIATION IN 73 CANES IN A The peaks in the weight of 73 canes per plot for area A at harvests 6 and 8 were non-significant and mainly the result, in each case, of one particularly dense plot. The large amounts of 73 canes were reflected in weights of 74 lateral and lateral leaves borne on them. Subsequent calculations of maximum summer biomass etc. for A are based on harvest 7 to avoid the distorting

Fig 5



—— 74 LATERALS +
LATERAL LEAVES

----- 74 CANES + CANE
LEAVES



effect of these dense plots. The level of 73 canes at H7 was similar to that for harvests 1-5.

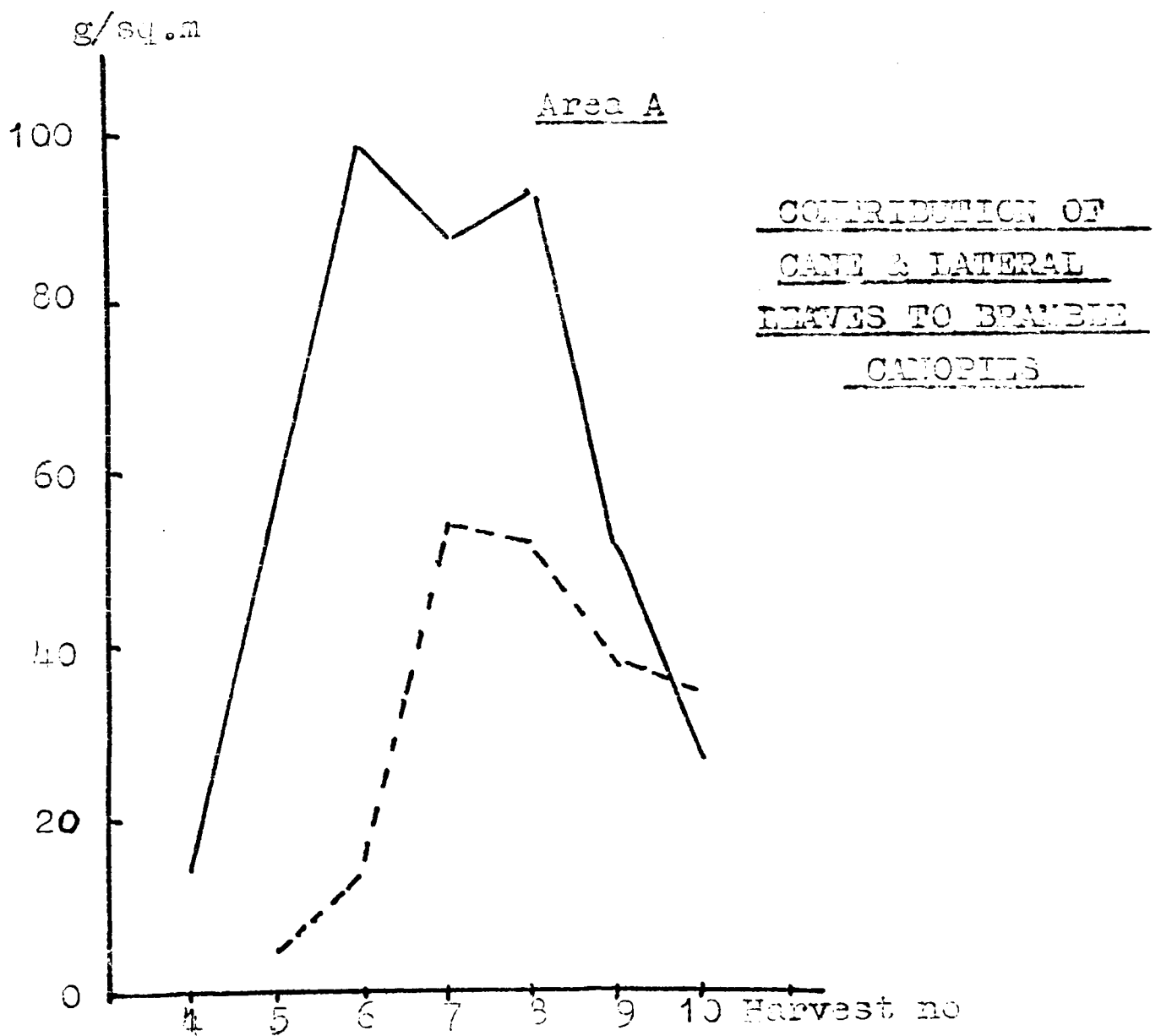
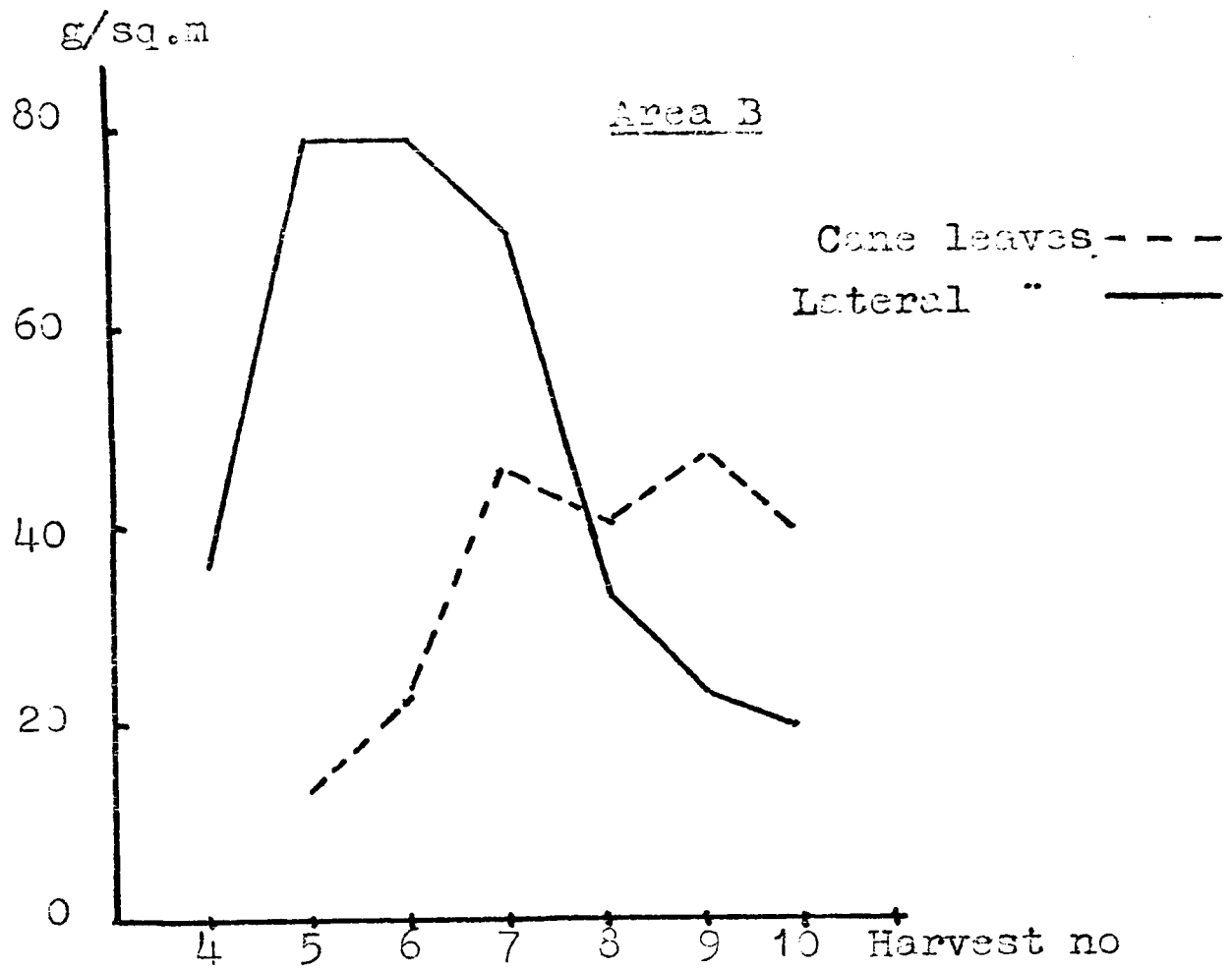
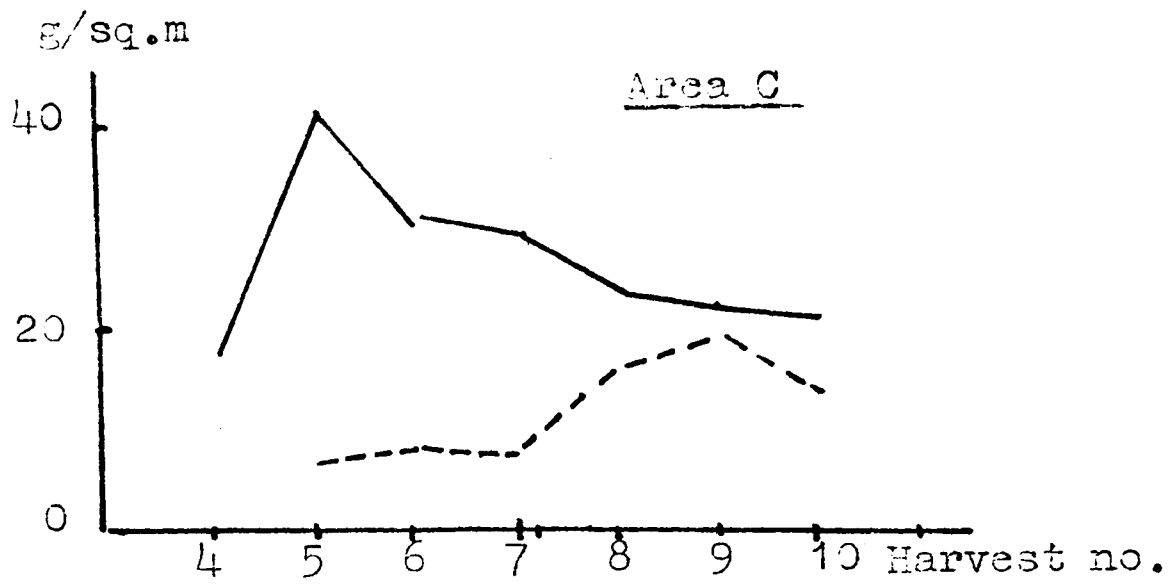
THIRD-YEAR CANE SYSTEM

68 **FINAL DIE-BACK** The death of the remains of the previous year's flowering cane-system occurred mainly during the early summer. In A little loss of weight occurred before new growth started in spring at H3. The same applied to loss of 73 lateral leaves from B and C, but the levels of stems were small compared to sampling errors so that it was difficult to detect any decline in weight of the stem components. The coincidence of the start of new growth and the recommencement of the decline in dry-weight of the dying components suggests that die-back might be an active process. Material withdrawn from the dying tissues could supply the new growth.

69 **"TERTIARY" GROWTH** A few canes in A survived until the autumn and these produced fresh laterals both directly on the 72 canes and on the 73 laterals. The contribution of these laterals to the total weight of new laterals per plot was small.

COMPARISON OF GROWTH BY FIRST AND SECOND-YEAR CANE SYSTEMS

70 **TIMING OF GROWTH** ^{P.24,25} Fig. 4 shows that the net increase in dry weight during the growing season was about the same in the second-year cane system as in the first. There was, however, a difference in the timing of growth by first-year canes compared with that by laterals (^{P.29} Fig. 5). The earlier start to growth by the laterals may be partly a sampling bias. Laterals were separated as a distinct component as soon as the buds opened. New canes, however, were not sampled until they had emerged from the layer of litter and moss on the ground.



71 There were many lateral growing points per second-year cane compared to only one growing point per first-year cane. Initial increase in dry-weight per unit area was thus more rapid for the laterals. Growth of the new cane continued into the late summer whereas lateral growth was limited by the formation of flowers. As a result much of the cane growth occurred after maximum dry-weight had been reached in the laterals.

72 LATERAL AND CANE-LEAF CANOPIES The two types of leaf made distinct contributions to the overall bramble canopy. The main increase in leaf dry-weight was from April to June, but the bulk of this was lateral leaves. Cane leaves did not reach maximum weight per plot until much later (P.31 Fig. 6). Although the amount of cane leaves was much less than that of lateral leaves, the cane leaves increased in importance in the winter canopy. Whereas there was little loss of cane leaves in the autumn, lateral leaves showed a large decrease.

73 Sykes and Taylor (In press) found a similar separation of cane and lateral growth in Rubus vestitus at Meathop Wood. By this separation competition between first and second-year canes on the same rootstock is reduced. Perhaps There is a more effective utilisation of available light because the cane leaves do not reach their maximum until just before or during the decline of the lateral leaves.

TOTAL BIOMASS

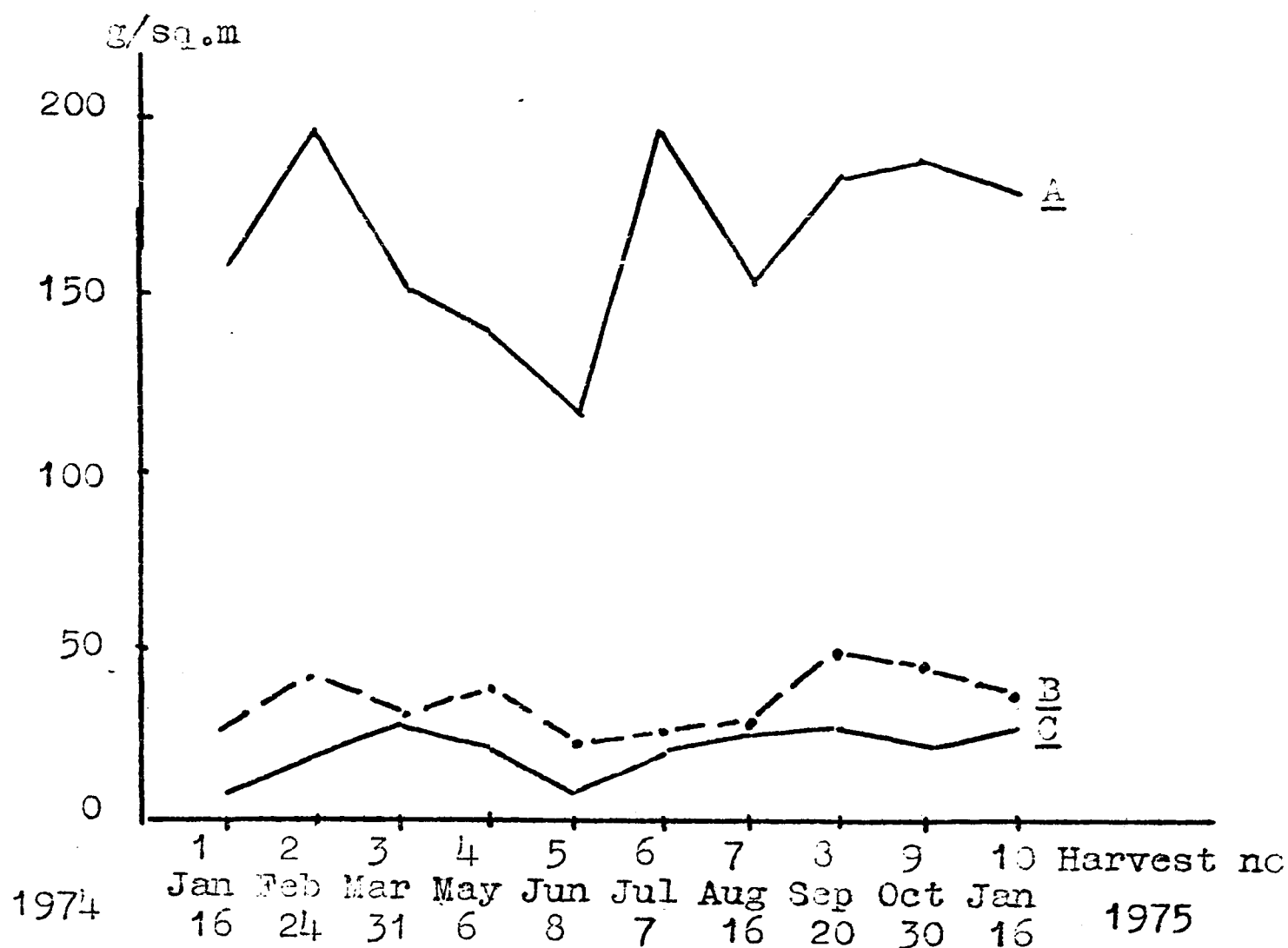
74 SUMMER PEAK All three areas showed statistically significant summer peaks in biomass (P.34 Fig. 7). The size of this summer increase relative to the winter biomass was similar for all three areas (P.33 Table 7).

TABLE 7

RELATIVE BIOMASS INCREASE
IN SUMMER

Table 7

	Area	A	B	C	
Winter biomass	263	150	90	g/sq.m	
Summer increase	175	127	59	"	
<u>Increase</u>					
Winter biomass	0.65	0.85	0.65		

STANDING DEADFIG. 3BIOMASSFIG. 7

75 CAUSE OF SUMMER PEAK Changes in total biomass were the resultant of changes in all the individual components, some of which increased, others decreased over the season. The size and timing of the summer peak was thus the combination of three processes:-

- 1) the increase in dry weight of first year canes.
- 2) the initial increase in weight of the second year cane system because of lateral growth followed by a decline as die-back occurred.
- 3) the decline in weight of the third year cane system through die-back. Peak biomass was earliest in C because the start of the decline in weight of the second year cane system occurred before that in A and B where there was greater overlap of cane and lateral growth.

STANDING DEAD

76 COMPOSITION This component was made up of canes and laterals that had recently died, and the more resistant parts of stems that had died some months before. No distinction was made between dead stems of different types and ages. Death of a stem was marked by it turning brown, presumably as a result of loss or breakdown of stem chlorophyll. Not all the losses in dry-weight from living components over the year, represented material entering the standing dead category. Most leaves fell straight to the litter layer. Some of the dry-weight loss from stem components was through respiration or translocation of material to the rootstocks or to leaves.

77 TURNOVER OF STANDING DEAD There was no statistically significant change in the level of standing dead during the course of a year(^{P.34} Fig. 8). Input from the death of canes or laterals was

TABLE 8

RATE OF TURNOVER OF
STANDING DEAD

Table 8

	Area A	B	C	
Dry weight losses from living stem components				
73 canes	50	39	9	g/sq.m/yr.
74 laterals	54	36	3	"
72 canes	65	12	12	"
73 laterals	50	8	8	"
TOTAL	219	95	32	"
Mean dry weight of standing dead				
	164	35.6	20.9	g/sq.m
<u>Standing dead</u> Live-stem loss	0.75	0.37	0.69	yrs.

TABLE 9

RELATIVE SIZE OF STANDING
DEAD COMPONENT

Table 9

	Area A	B	C	
Winter biomass	263	150	90	g/sq.m
Standing dead	164	35.6	23.2	"
<u>Standing dead</u> Winter biomass %	62	24	23	

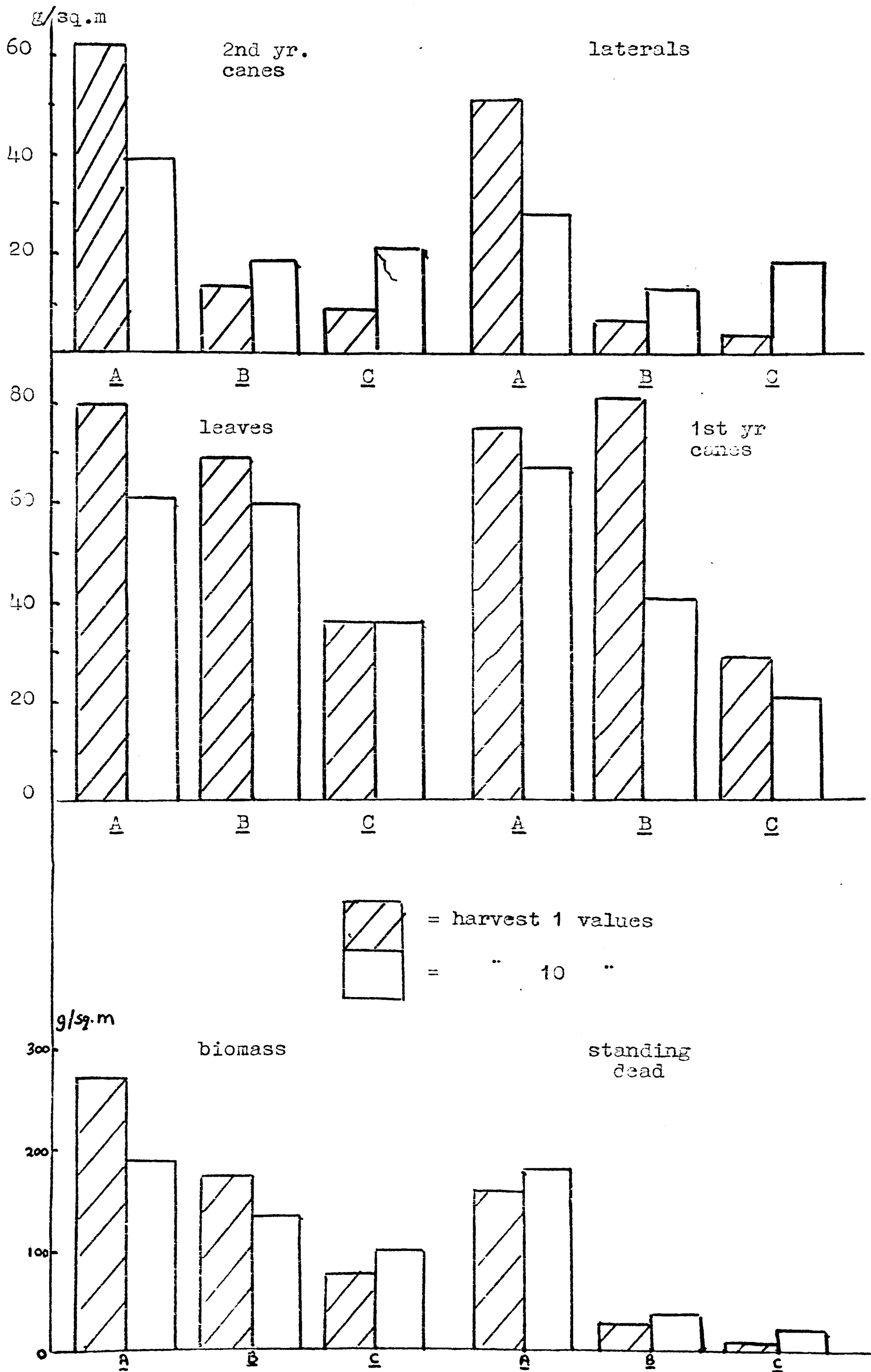
thus matched by standing dead falling to the litter or being decomposed in situ. If it is assumed that the bulk of the net decrease in the weight of each live stem component over the year passed through the standing dead stage, it is possible to estimate the turnover time for standing dead(^{P.36} Table 8) Because of the various other ways in which dry-weight can be lost actual input would have been less than in Table 8, i.e. the turnover time is longer than given here.

78 FASTER TURNOVER IN AREA B On these figures the rate of turnover of standing dead was about twice as fast in B as in areas A or C. There was no apparent reason for this. Possibly the microclimate near the ground was moister than in A or C as a result of a dense, low tree canopy, and a continuous bramble cover. This might lead to the faster rates of decomposition observed in B.

79 RELATION OF STANDING DEAD TO WINTER BIOMASS. ^{P.36} Table 9. A had a much higher weight of standing dead compared to winter biomass, relative to B or C. A had a higher stem:leaf ratio than B or C so that potential input to standing dead, relative to the winter biomass, was much greater. B produced relatively more stem than leaf compared to C, but this was offset by the faster turnover for standing dead in B. Relative to winter biomass therefore, the standing dead amounts were similar in B and C.

YEAR-TO-YEAR VARIATION

80 Harvests 1 and 10 both took place in January. A comparison of equivalent components for the two harvests may indicate how much variation there was between growth in 1973 and that in 1974 ^{P.38} Fig 9). Growth of first year canes was lower in 1974 than in 1973, but the



difference was statistically significant only in B. Survival of second year canes and their laterals overwinter was greater in B and C but less in A. Either conditions for die-back were less favourable in B and C in autumn 1974 compared to 1973 (more favourable in A) or growth of these components was greater in 1974 (less in A) than in 1973. These differences in growth and die-back were probably caused by variations in the weather. Differences between equivalent components at the beginning and end of the year were less than the variations in component dry-weights over the year.

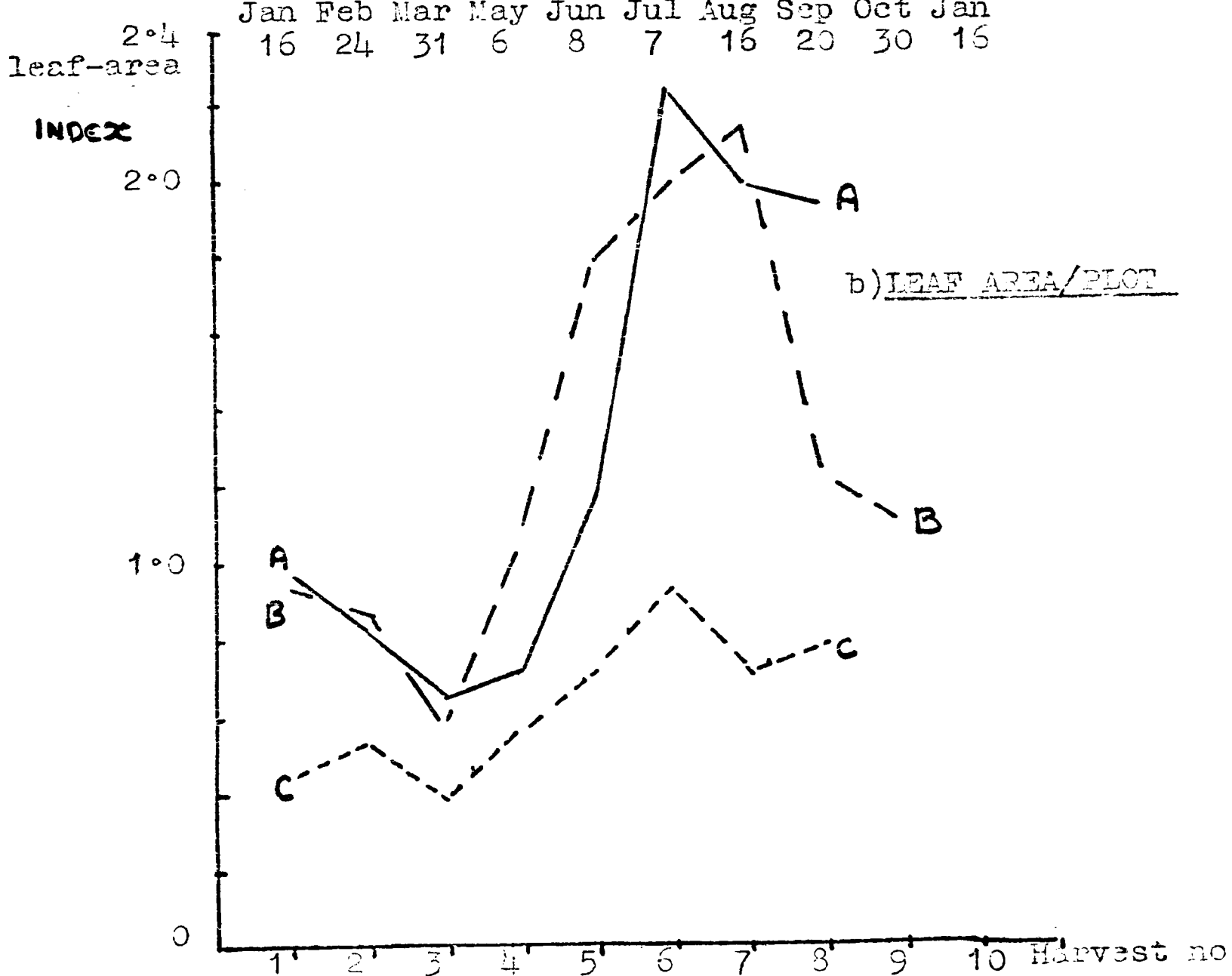
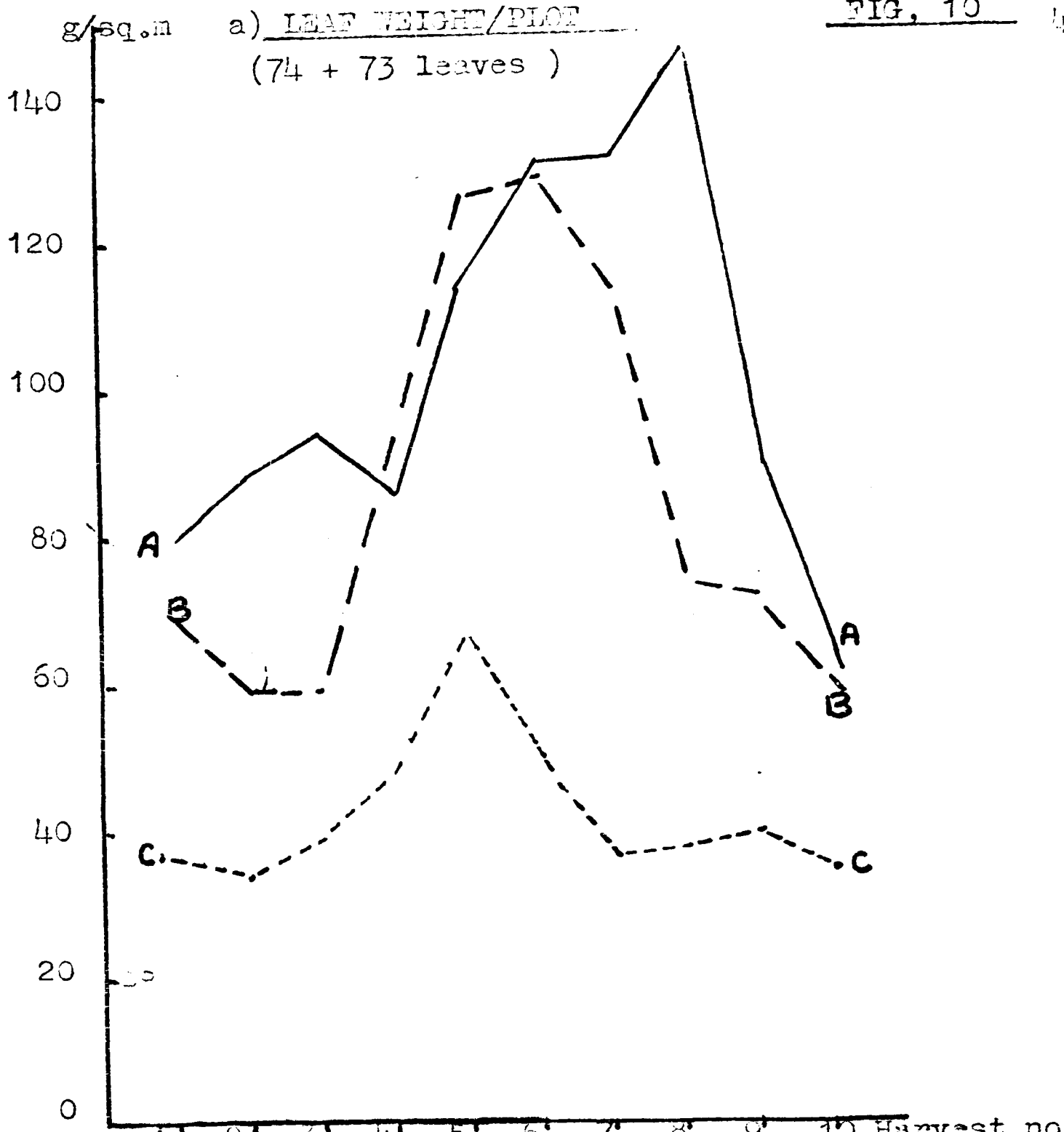
DIFFERENCES IN GROWTH TIMING BETWEEN AREAS

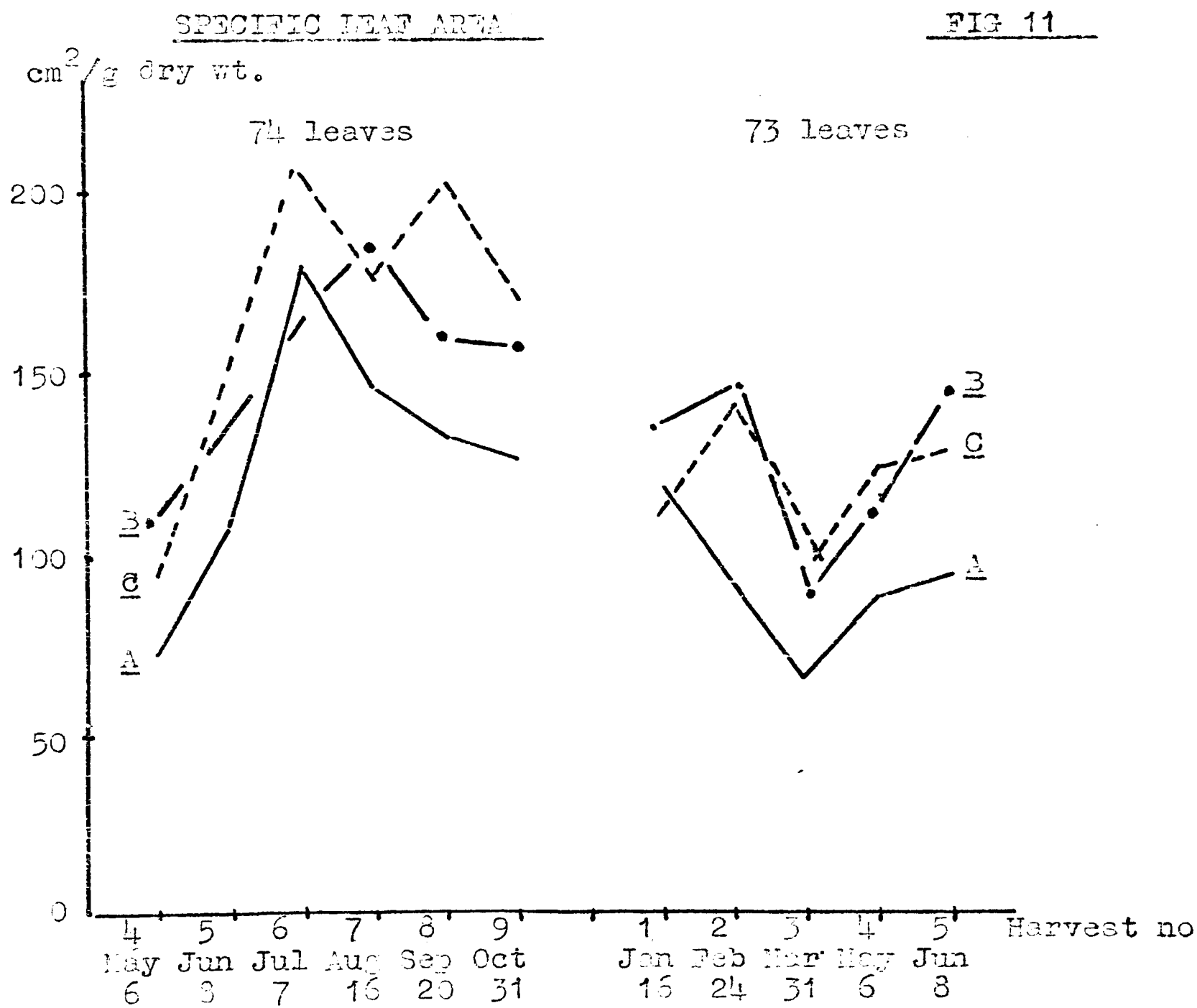
81 START OF GROWTH In 1974, and the two subsequent years, growth started later in spring in A. Growth appeared to be 3-4 weeks behind that in the other two areas and it took 8-10 weeks for the difference to be made up. A was on the north-facing slope of the hill while C faced west and B south-west. The less-favoured aspect of A may have delayed its start of growth.

82 AUTUMN DIE-BACK B showed greater autumn die-back than C or A. Thus although the weight of the second-year cane system was much greater than in C during the summer, the weight of canes and laterals surviving over winter was the same in B as in C. The reason for the greater autumn die-back is not known, nor whether it is connected with the faster turnover of standing ^{dead} in B.

LEAF COVER

83 SUMMER AND WINTER BRAMBLE CANOPIES. ^{P.40} Fig 10. The summer bramble canopy was about twice that in winter, but at no time was there no leaf on the bramble stand. The leaf-area-^{index} of about





2.0 for A and B in summer was sufficient to give virtually complete leaf cover because leaf angles were low. Even in summer, however, in C, the bramble canopy was not continuous.

84 This partial evergreenness may have a number of advantages for the plant. It may allow photosynthesis to take place in autumn, winter and early spring when the leaves are off the trees. The presence of old leaves in the spring may be particularly useful because they could make use of any favourable conditions that occur before the new bramble canopy has had a chance to develop. The all-year-round canopy reduces the opportunities for species growing beneath a bramble stand. Even where a species grows in the spring before the leaves are on the trees, the light reaching it is reduced by the presence of bramble leaves.

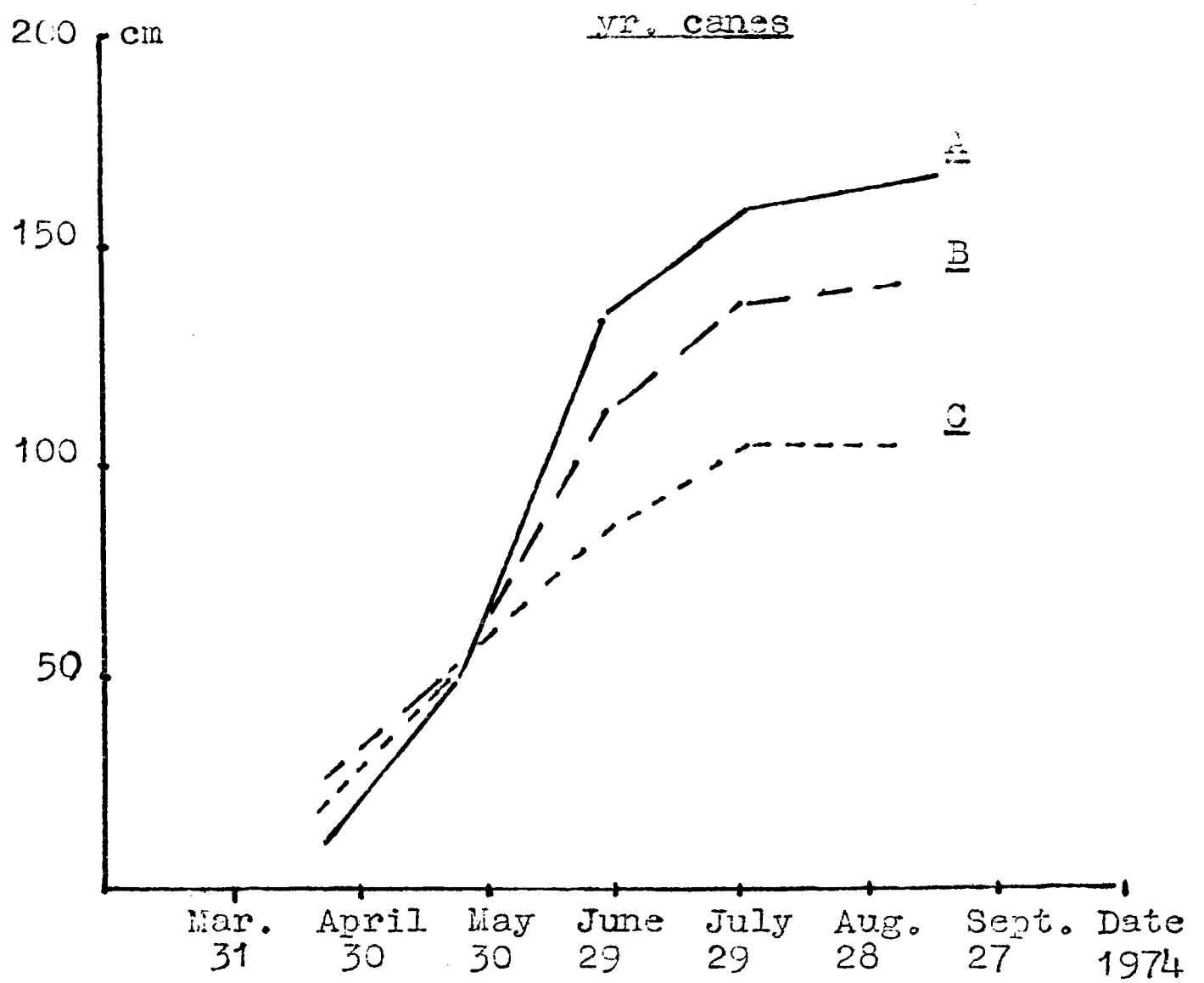
85 SIMILARITY OF A AND B CANOPIES The differences in leaf dry-weight per unit area and in leaf-area^{-index} for B and A were small compared to the differences in total dry-weight per unit area. The increased growth in A must have been brought about by greater photosynthetic activity per unit of leaf.

86 SPECIFIC LEAF AREA ^{P. 42} Specific leaf area, Fig. 11, was rather variable because of the relatively small samples used in the measurement of leaf area. A showed the lowest S.L.A. i.e. the heaviest leaf weight per unit area which fits with the greater carbohydrate production suggested in the previous paragraph. Expansion of 74 leaves, H4-6, caused the rise in S.L.A. during this period.

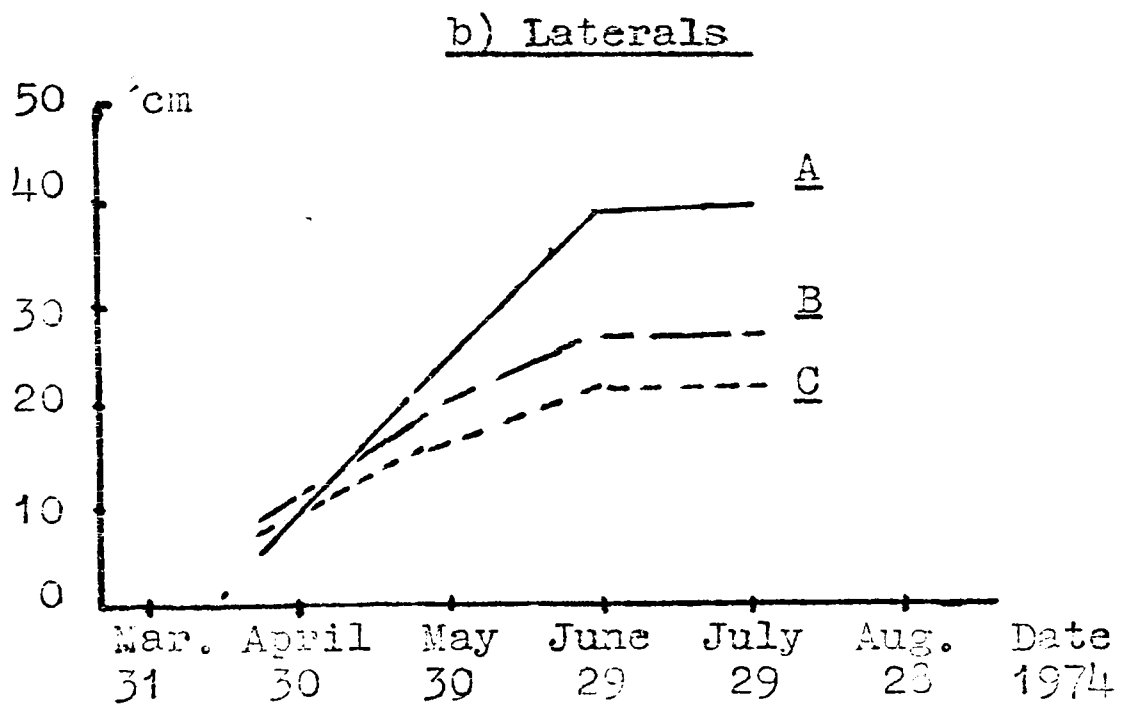
CHANGES IN STEM LENGTH OVER THE YEAR

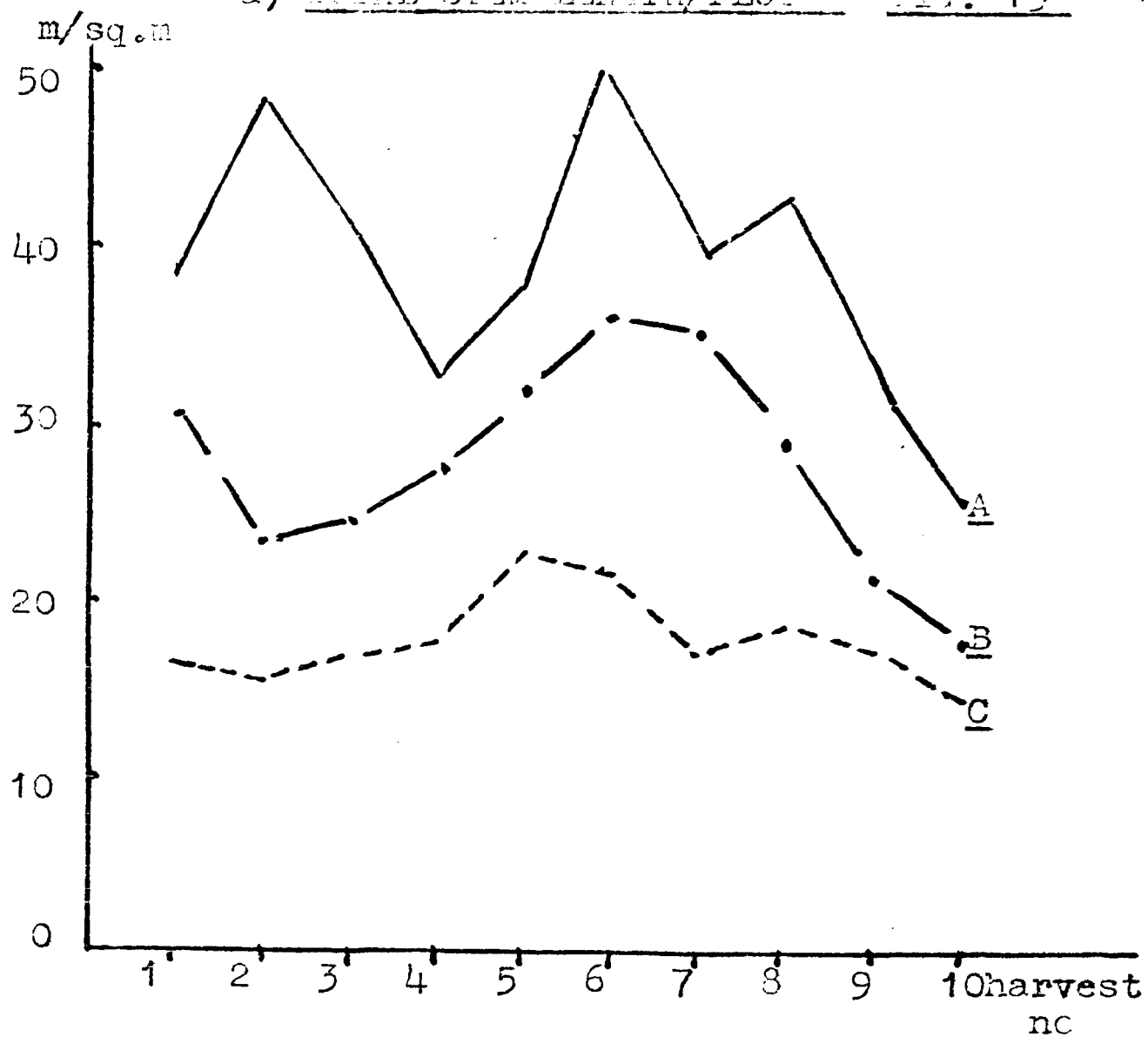
87 FIRST-YEAR CANES. ^{P. 43} Fig. 12. The pattern of growth in length of individual canes was the same for all three areas and similar to

FIG. 12

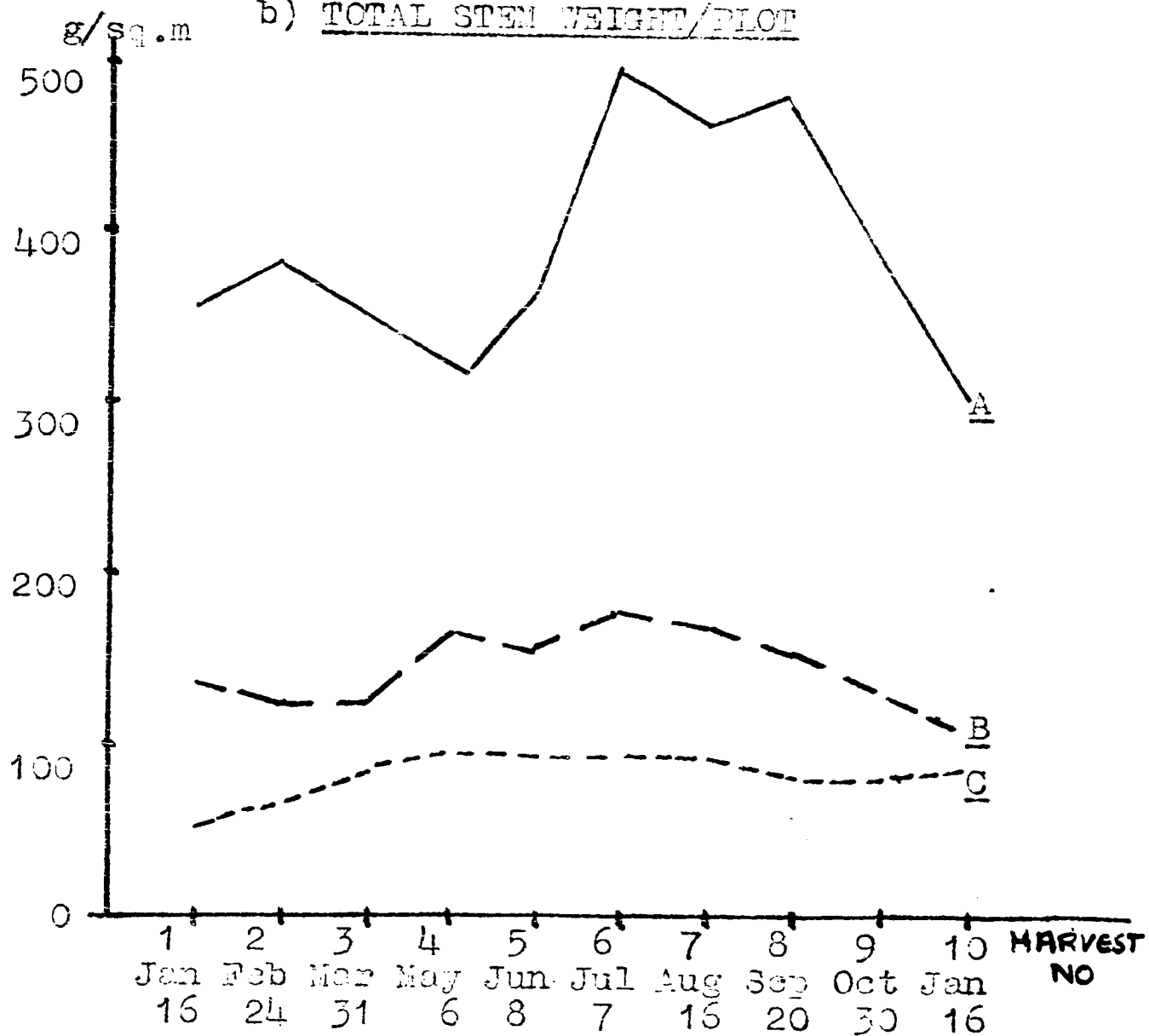


GROWTH IN LENGTH OF INDIVIDUAL STEMS





b) TOTAL STEM WEIGHT/PLOT



the increases in dry-weight. This suggests that the main source of increased dry-weight was growth in cane length. The duration of the growing season was similar for both length and weight increase ^{P.46} (Table 10). Small differences in the time of beginning and end of growth were caused by the times at which measurements were taken.

88 **LATERALS** There was similar agreement between the pattern of length and dry-weight increase for laterals. Extension of laterals ended, about a month before that of the canes, with the formation of inflorescences. Although the sample size for both cane and lateral measurements were small, five 74 canes and five 73 canes in each area, they show that there were differences in plant size between the areas, as well as differences on a unit area basis.

89 **TOTAL STEM-LENGTH/sq.m** Total stem-length per metre-square rose to a peak in the summer for all three areas, because of the growth of new canes and laterals(^{P.44} Fig. 13). Variation in A was greater than in B or C, because the greater amounts of stem present in A made measurements more difficult. Curves for total stem length for B and C bear the same relation to each other as the curves for total stem dry-weight. There is, however, a much greater difference in stem-weight between A and B than in stem length. This was because while stem diameters in B and C were similar, those in A were much greater.

PLANT DENSITY

90 **ROOTSTOCKS/sq.m.** There was no statistically significant variation between harvests in the number of rootstocks per plot. ^{P.46} (Table 11). The differences between areas were significant although small compared to the differences in dry-weight per plot between A, B and C.

TABLE 10

DURATION OF GROWTH

Table 10

	Area	A	B	C	
Canes					
Weight increase		106	122	117	days
Length increase		106	126	121	"
Laterals					
Weight increase		90	82	82	"
Length increase		75	94	90	"

TABLE 11

PLANT DENSITY

Table 11

	Area	A	B	C	
Rootstock nos		3.1 ±0.2	3.8 ±0.2	2.7 ±0.2	per sq.m
Canes		9.0 ±0.5	10.1 ±0.5	7.2 ±0.5	"
Canes/rootstock		2.9	2.7	2.7	

91 CANES/sq.m. The differences in cane numbers per plot between A and B were not significant, but both were significantly higher than the cane density in C. Numbers of canes per rootstock were, however, similar for all three areas.

92 AGE DISTRIBUTION OF CANES Most rootstocks produce a new cane every year. Therefore a distribution of one first-year, one second-year, one dead or dying third-year cane per plant was expected. This could not be shown for the harvest plots because the canes were not classified by age.

93 For five metre-square plots in each area the canes present on each rootstock in March 1974 were separated into age classes^{P. 48} (Table 12). Despite the similarity in total cane numbers per unit area for B and A, the age structure of canes on a rootstock was very different. First-year canes were a much higher proportion of total numbers in B.

94 TURNOVER OF CANES Each year a set of canes equivalent to the number of first-year canes become standing dead. These can be compared with the number of canes currently in the standing dead to obtain an estimate of the turnover time for this category, as was done with dry-weights, ^{P. 48} page 37. Table 13 shows the two methods give similar results although the dry-weight values are lower. As was pointed out, however, the dry-weight figures give only a minimum turnover time.

PARTITIONING OF DRY WEIGHT BETWEEN COMPONENTS

^{P. 48}
95 LEAF: STEM Table 14. A had a lower leaf:stem ratio than B or C because of the greater diameter of stems in A. For the same reason, canes in all three areas had lower leaf:stem ratios than laterals. Thus in the second year a greater proportion of the dry-weight increases went into leaf formation.

TABLE 12

AGE DISTRIBUTION
OF CANES

Table 12

Area	A	B	C	
1st yr. canes	1.0	1.34	1.07	per rootstock
2nd " "	1.0	0.17	0.41	" "
Dead canes	1.1	0.62	0.85	" "

Based on rootstocks found in 5 metre-square plots per area in March 1974.

TABLE 13

TURNOVER TIME FOR
STANDING DEAD

Table 13

Area	A	B	C	
From Table 8	0.75	0.37	0.65	yrs. Based on dry weight changes.
From Table 12	1.10	0.46	0.79	" $\frac{\text{no. dead canes}}{\text{no. 1st yr. canes}}$

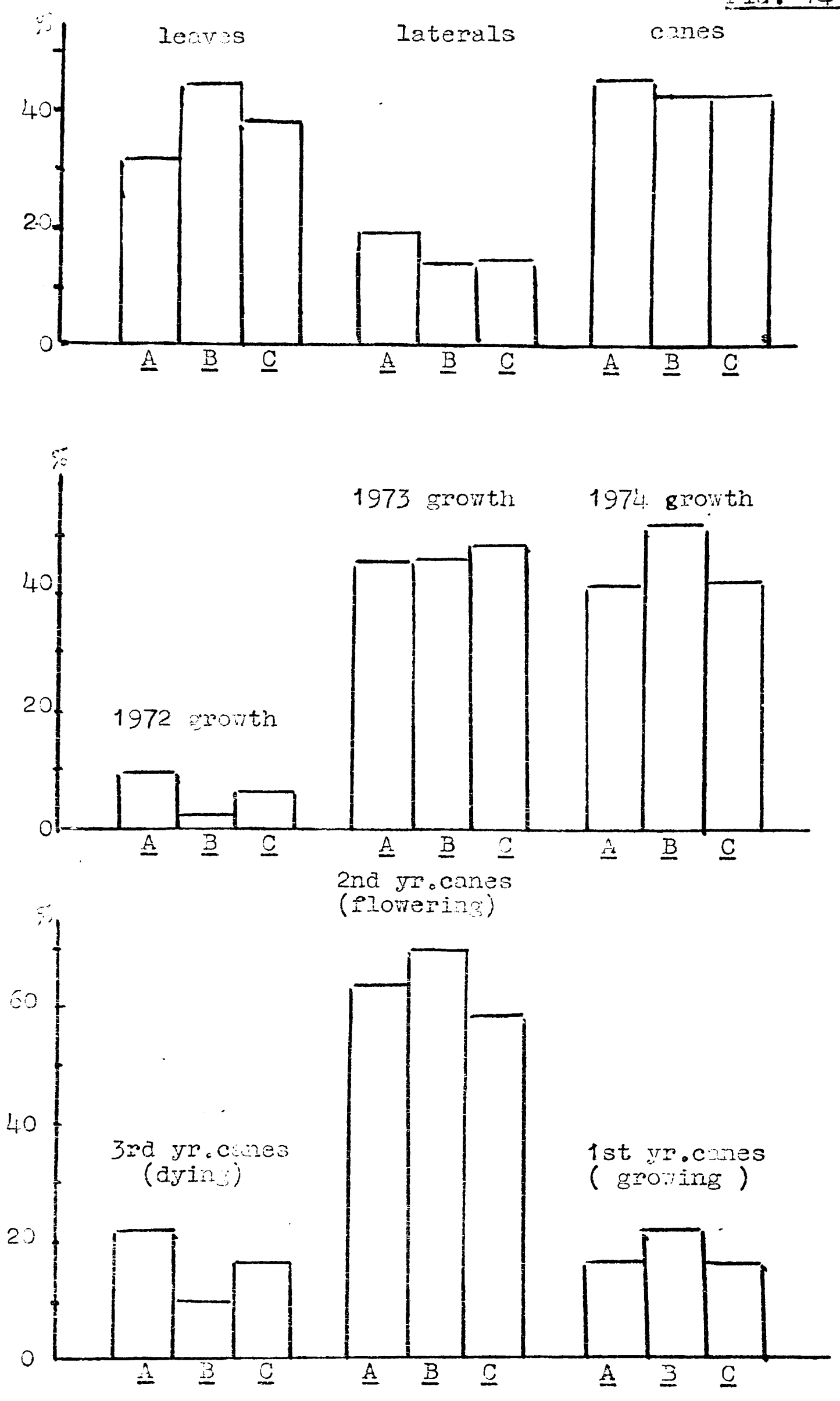
TABLE 14

LEAF-STEM RATIOS

Table 14

Area	A	B	C
Canes	0.75	0.96	1.04
Laterals	0.94	1.61	1.95

Based on dry weights of leaf and stem when canes/laterals fully grown.



CONTRIBUTIONS TO MEAN BLOCK BIOMASS
OVER THE YEAR

96 MEAN BIOMASS OVER THE YEAR By combining the results from all the harvests the mean biomass over the year was calculated.

The contribution of different components to this value was a function of the length of time they were present as well as the maximum dry-weight reached. ^{P.49} Fig. 14 shows three ways of grouping the % contributions of the different components to this value.

97 (1) Into leaves, canes and laterals. The stem components in A made a greater contribution than in B or C because of its lower leaf:stem ratio. The leaf:stem ratio in B was lower than in C, but this was offset by the faster die-back of older canes in B in the autumn. This reduced the % contribution of stems. Laterals were present only in the second and third-year cane systems so that their contribution was less than that for canes or leaves.

98 (2) According to the year in which a component was formed, all 74 components together, all 73 components, all 72 components. The contributions of material formed in the current year and in the preceding year were nearly equal. Older material contributed less than 10% of the mean biomass over the year as a whole.

99 (3) According to the cane system ^{P.22} (Fig. 3) to which the components belong. The second-year cane system clearly made the greatest contribution to the yearly biomass. That of the developing first-year canes was about the same as the contribution of the canes that were dying back.

RELATIONS BETWEEN WEIGHTS OF DIFFERENT COMPONENTS

100 LEAF AND STEM WEIGHTS PER PLOT During growth the weight of leaves per plot was closely related to the weight of the stem fractions on which they were borne ^{P.51-53} (Figs 15, 16). The main weight

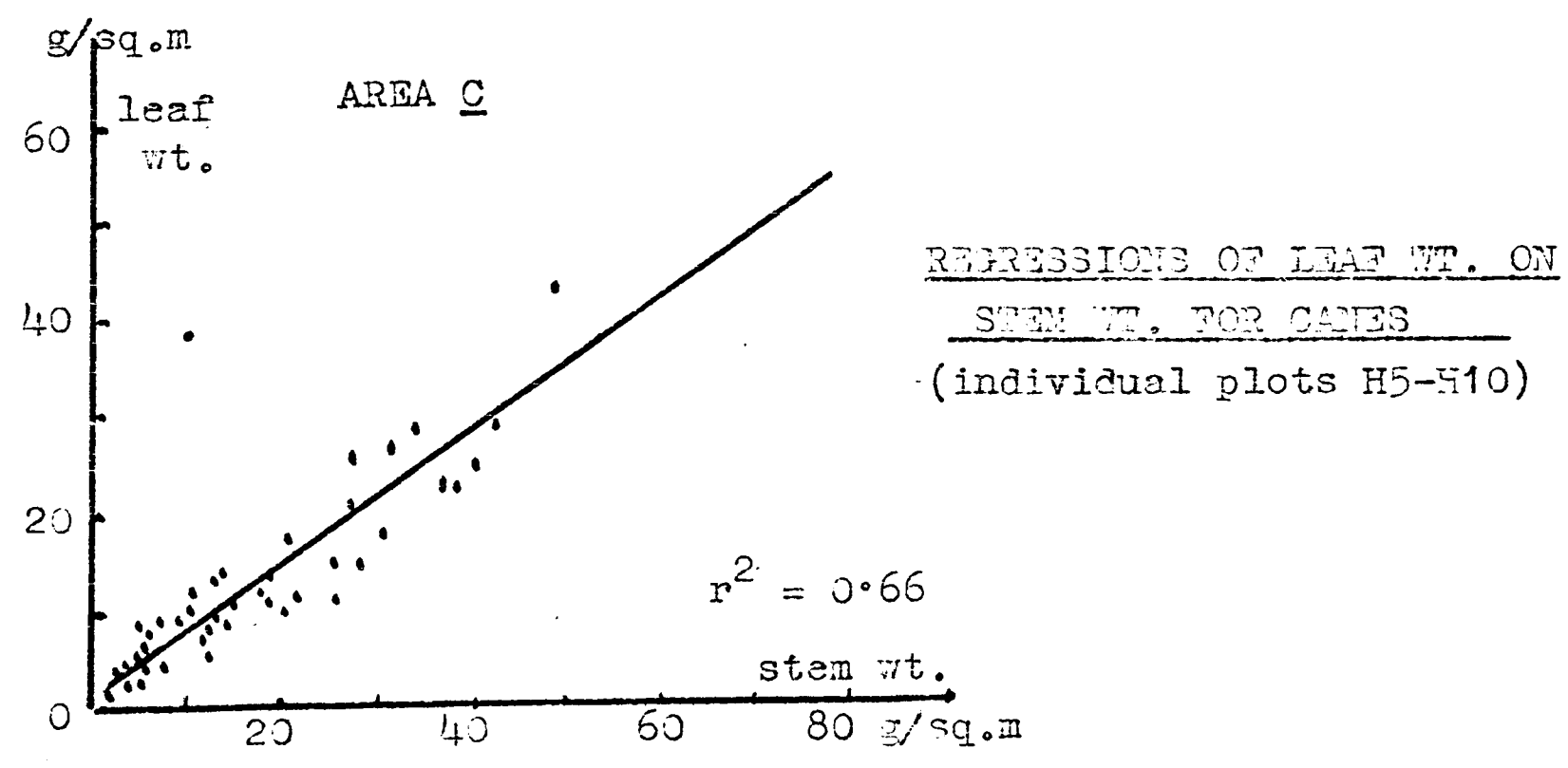
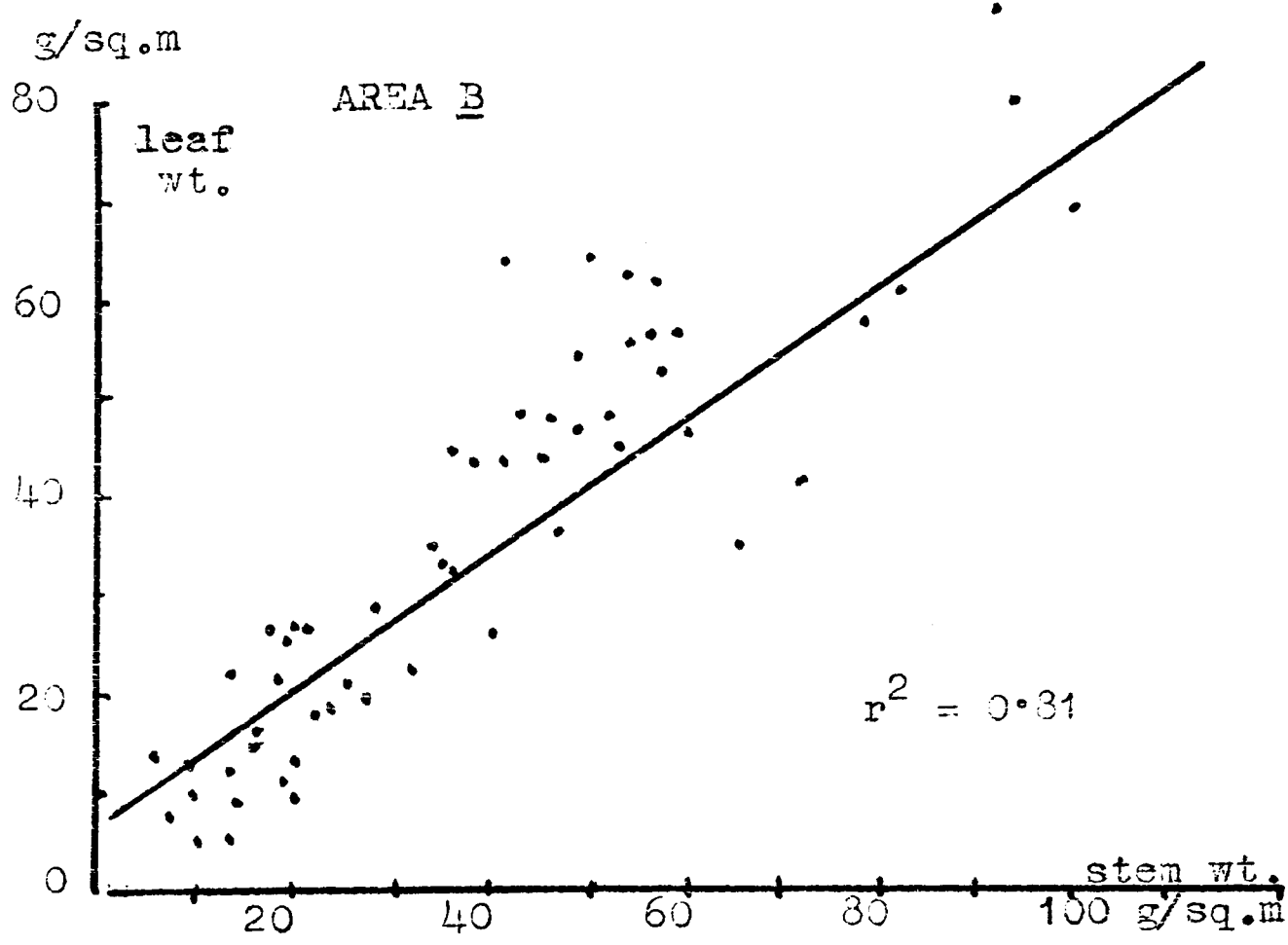
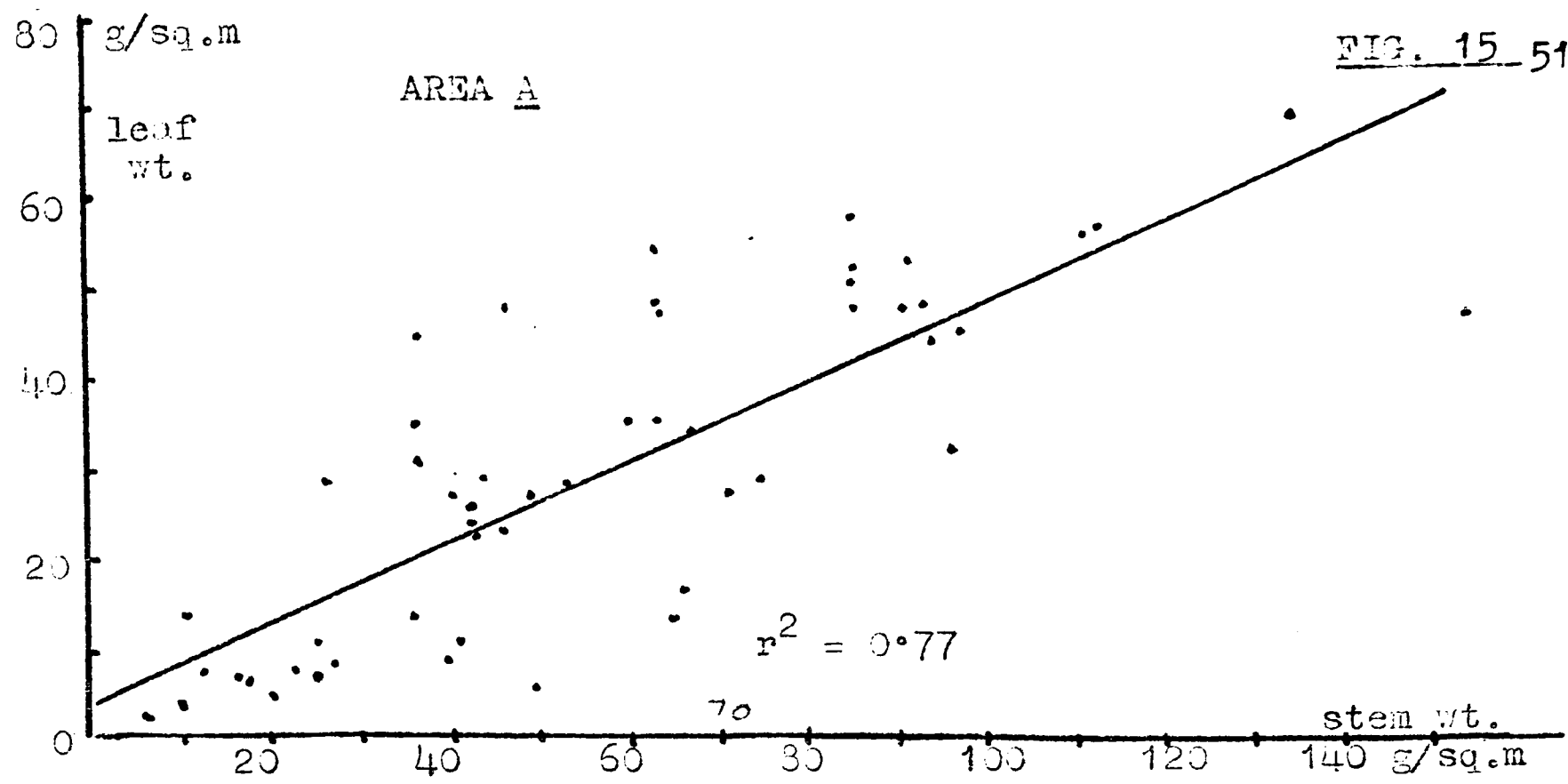
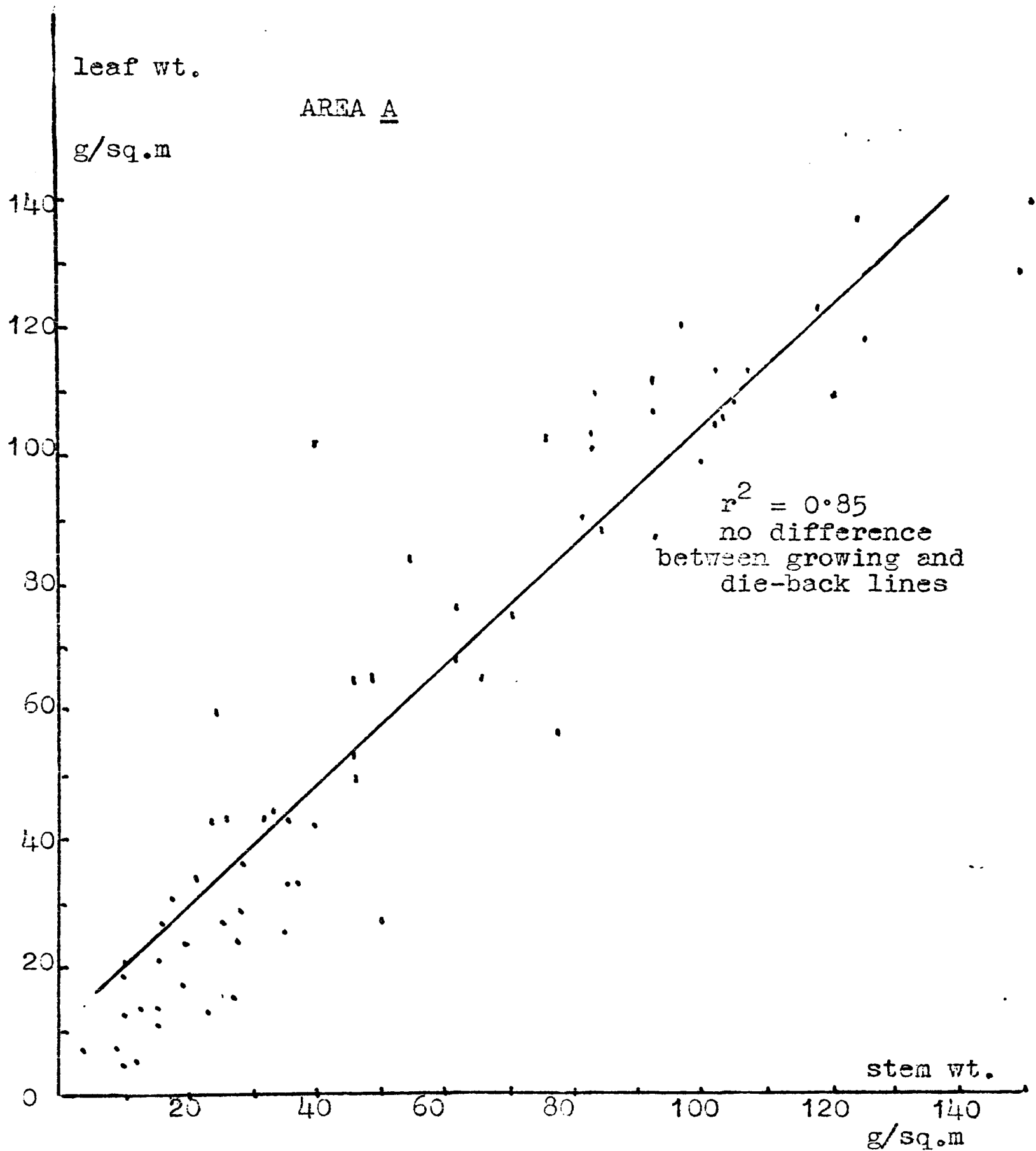


FIG 16

REGRESSION OF LEAF WT. ON STEM WT. FOR LATERALS

(individual plots H4-H10)

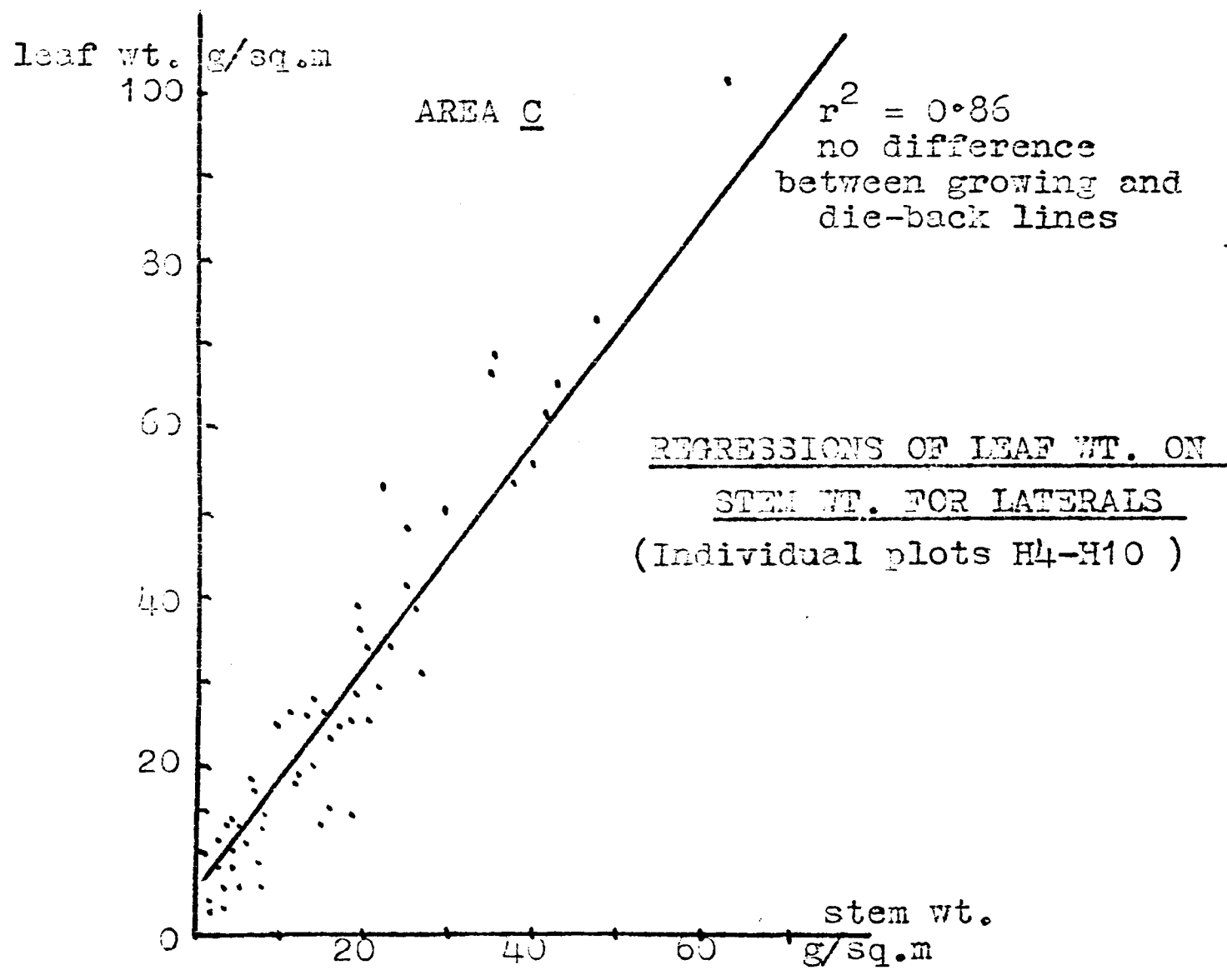
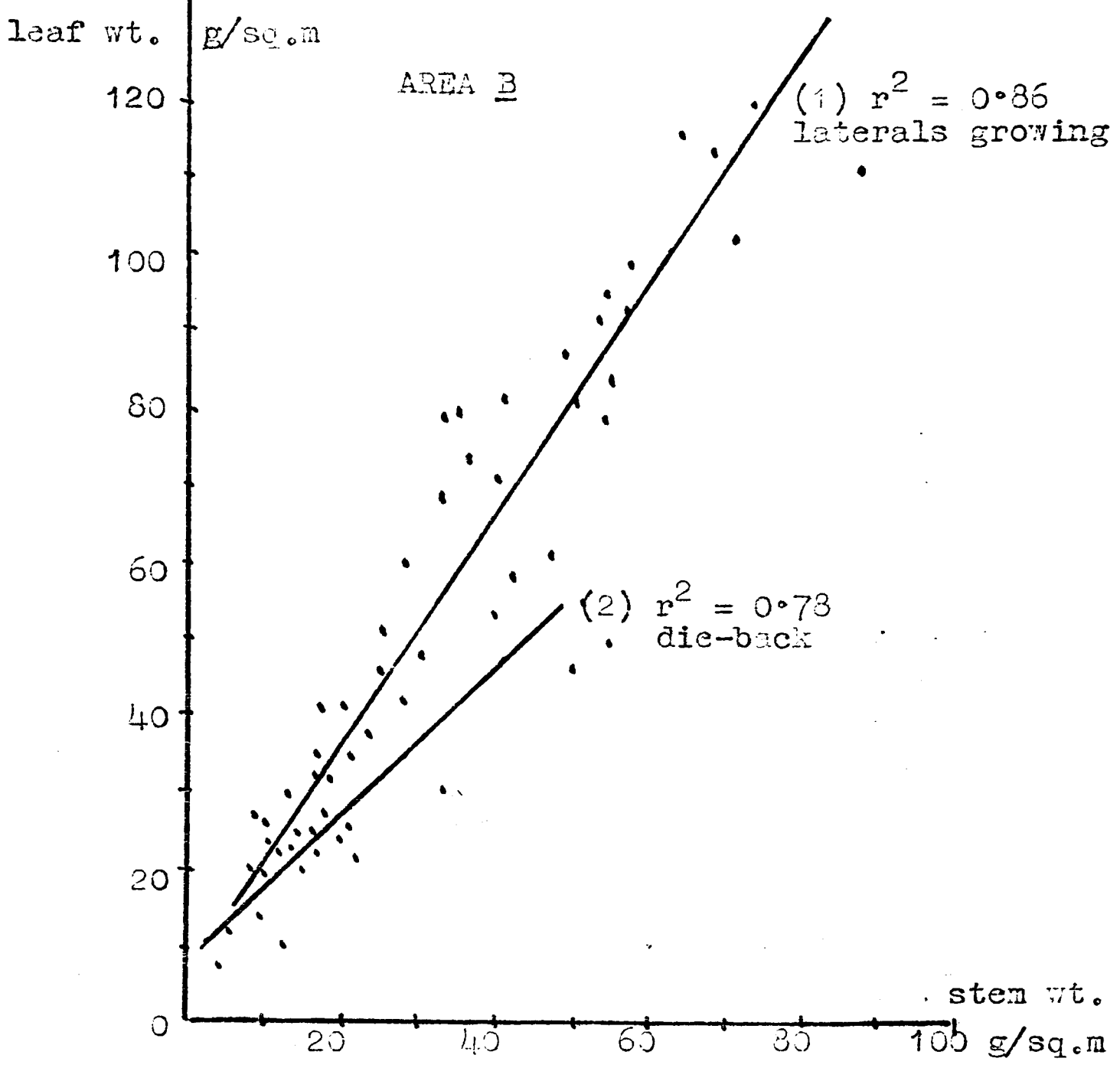
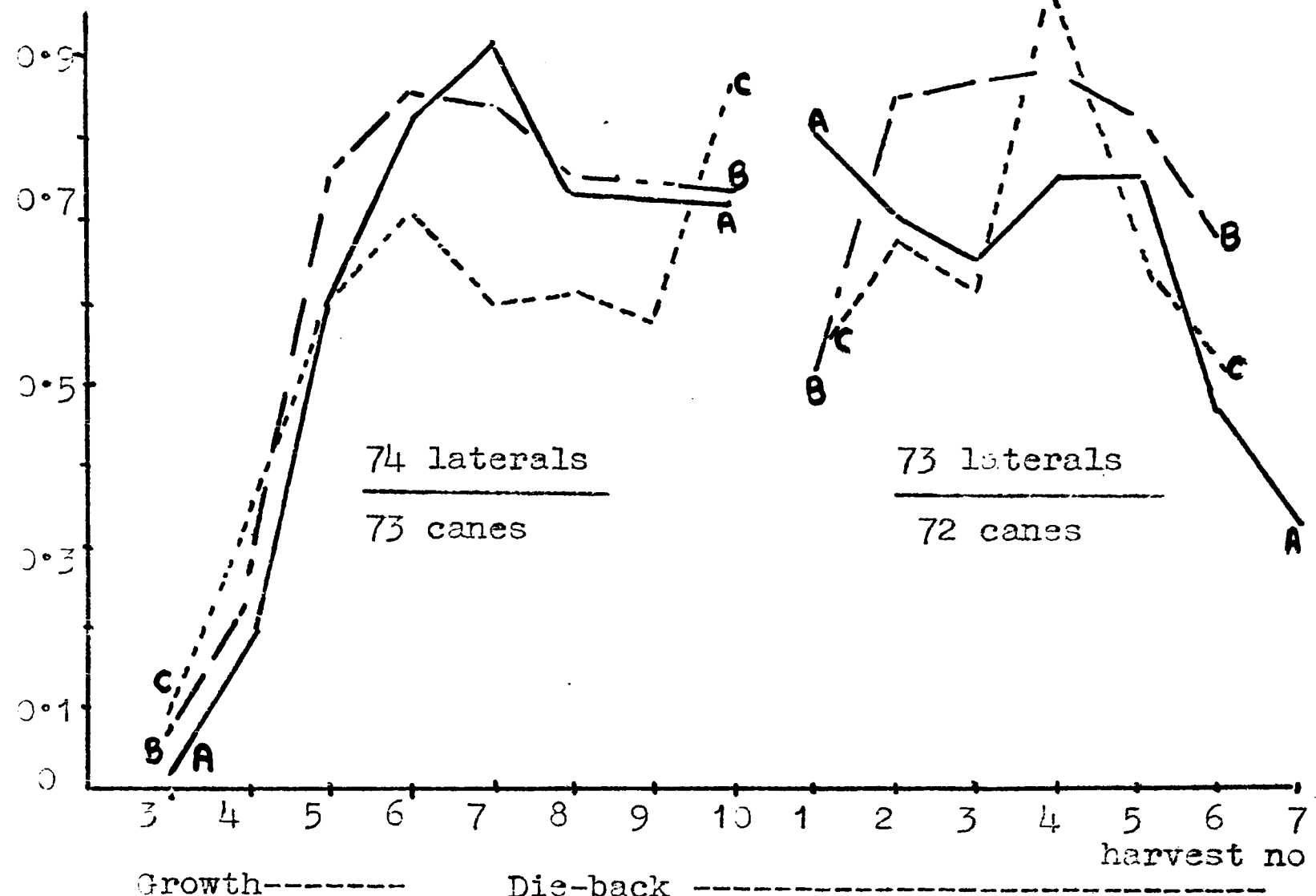


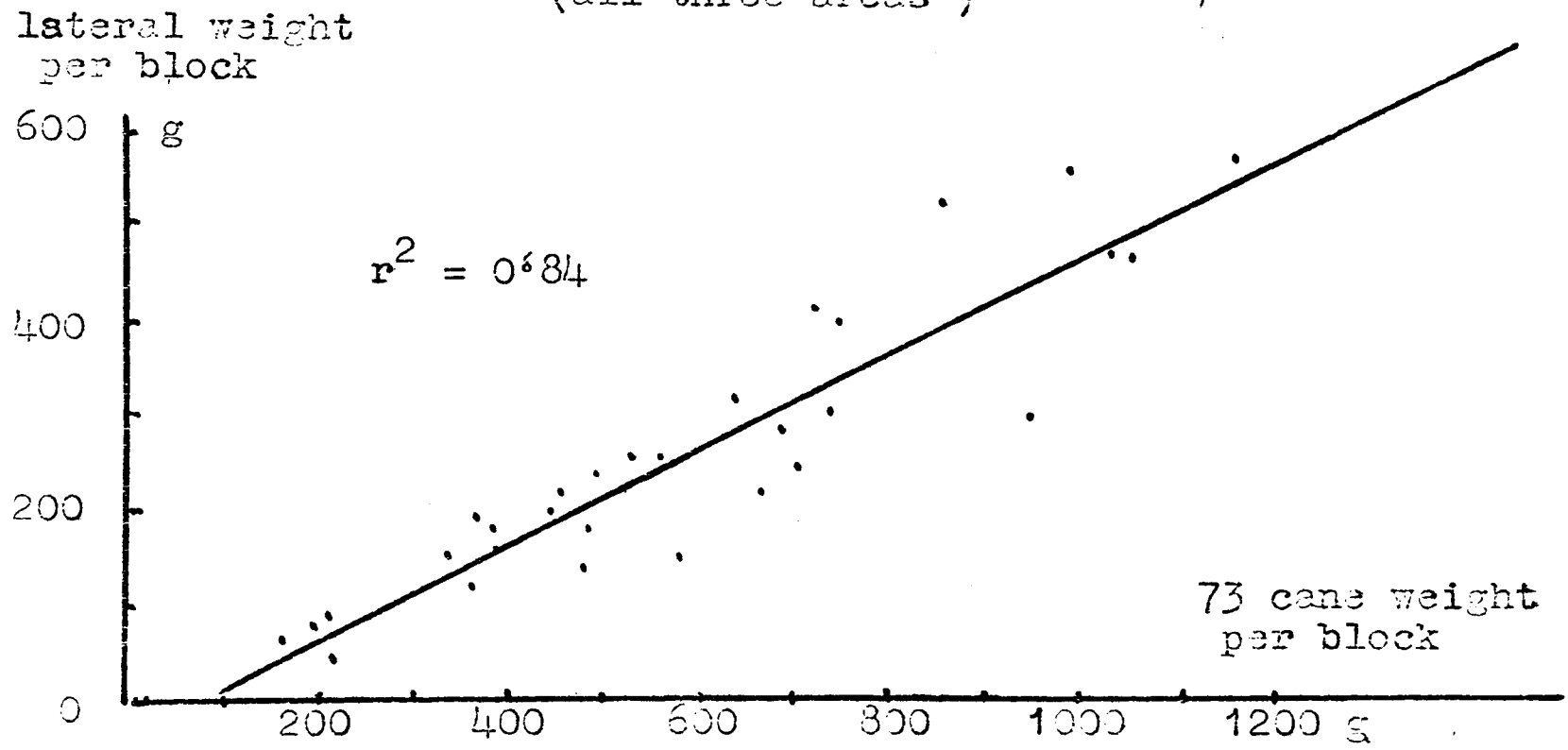
FIG. 17

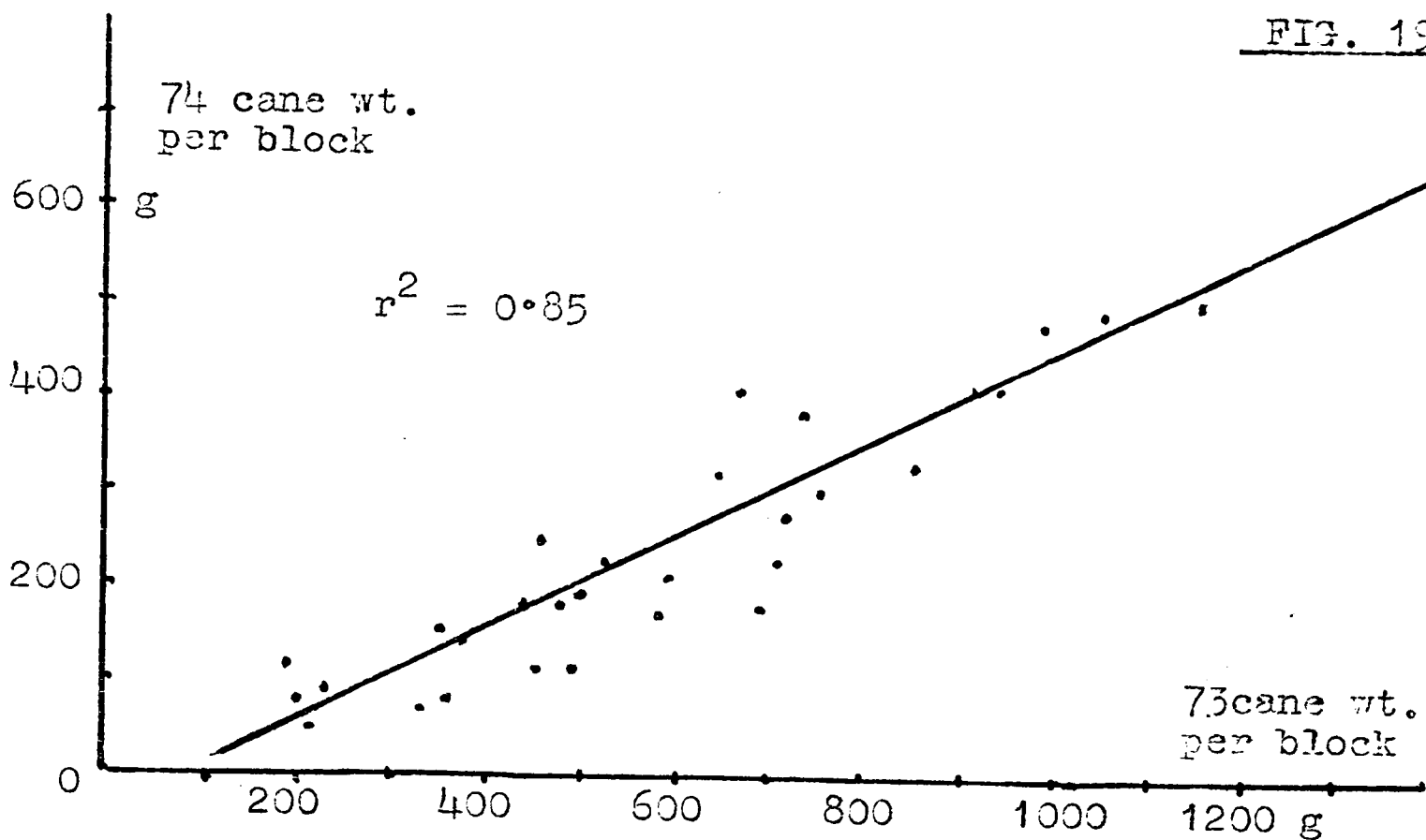


LATERAL WT.: 2ND YR. CANE WT.
DURING GROWTH & DIE-BACK

FIG. 18

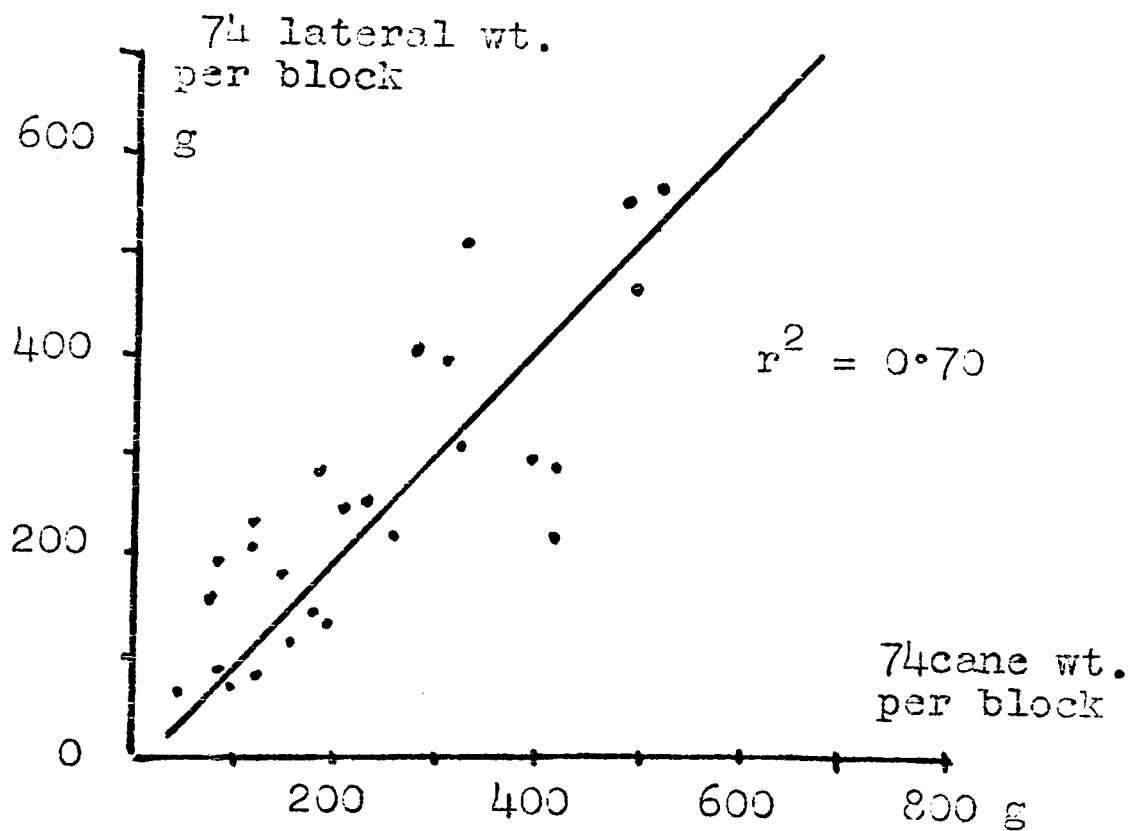
REGRESSION OF 74 LATERAL WTS. ON 73 CANE WT.
(all three areas)





REGRESSION OF 74 CANE WT. ON 73 CANE WT.
(all three areas)

FIG. 20



REGRESSION OF 74 LATERAL WT. ON 74 CANE WT.
(all three areas)

increase in stems was by increase in stem length, which was accompanied by further leaf development. At the same time there was little loss of leaves from the lower regions of the stems.

101 The relation between leaf and stem weight during increase in lateral weight was not very different from that for decrease in lateral weight(^{P. 52-53} Fig. 16). The loss of leaf weight was mainly caused by die-back of whole sections of laterals and their associated leaves, rather than death of leaves independently of lateral death.

102 LATERAL AND CANE WEIGHTS PER PLOT The ratio $\frac{74 \text{ lateral wt. per plot}}{73 \text{ cane wt. per plot}}$

increased rapidly during growth of the laterals because cane weights showed little change(^{P. 54} Fig. 17). After lateral growth ended the ratio remained fairly constant through most of the period of die-back of stems.

As with the leaf situation above, the loss in weight of live laterals per plot was accompanied by live-cane loss in weight, because whole sections of canes with their associated laterals died back at once.

103 74 LATERALS, 73 CANES, 74 CANES. WEIGHTS PER BLOCK Mean weights per block over the year were found for these three components by combining the results from all harvests.

74 laterals were borne on 73 canes. An increase in weight per block of the latter resulted in higher lateral weights(^{P. 54} Fig. 18).

74 canes were derived from the same rootstocks as 73 canes and subject to the same local environment, apart from year-to-year variations in conditions. A strong correlation between the two year's growth resulted(^{P. 55} Fig. 19).

74 cane weight and 74 lateral weight were also positively correlated(^{P. 55} Fig. 20). At the block level therefore, there was no evidence that high growth of laterals inhibited growth of new canes in the same area.

TABLE 15

SUMMARY OF DIFFERENCES
BETWEEN A,B,C.

Table 15

	Area	A	B	C	
Summer biomass		438	277	149	g/sq.m
Winter "		263	150	90	"
Rootstock no.s		3.1	3.8	2.7	per sq.m
Stem no.s		9.0	10.1	7.2	"
Summer leaf wt.		146	128	67	g/sq.m
Winter " "		71	65	36	"
Summer leaf area		2.23	2.14	0.92	leaf area index
Winter " "		0.97	0.94	0.44	" " "
Duration of growth					
Canes		106	123	119	days
Laterals		82	88	86	"

DISCUSSION

DIFFERENCES IN AREAS IN OVERALL GROWTH

104 NUMBERS AND SIZE OF PLANTS There was increasing biomass per unit area from area C to A (^{P.57} Table 15). Dry weights of most components increased similarly. Such differences were brought about both by differences in the number of plants and in the size of plants between the three areas.

105 LEAF COVER The increase in growth in B compared to C was brought about by a doubling of the quantity of leaves per plot with little change in the overall leaf:stem ratio. Between B and A, however, the increase in growth must have been largely a result of greater photosynthetic activity per unit of leaf. Growth rate rather than duration of growth changed between the three areas.

106 Other differences between the three areas occurred, such as in flowering and fruiting, the level of standing dead, the amount of autumn die-back. These may have been caused by the differences in overall level of growth between the three areas. More likely they were a result of environmental factors acting directly on the processes concerned.

ENVIRONMENTAL DIFFERENCES BETWEEN AREAS

107 TREE COMPETITION The canopy in A, ash, was the most open and allowed the greatest penetration of light and rainfall. That of C which included a large amount of sycamore was the most dense. This difference in tree canopy density was probably a major cause of the variation in bramble growth between the areas. Differences in below-ground competition between the trees and bramble may also have been responsible.

108 There was evidence that tree and shrub competition was controlling within-area variations in growth. Block 10, area A, had the lowest rootstock density and mean biomass over the year. Shrub cover within this block was higher than over the rest of the area. In B the bramble cover under a region of almost continuous hazel understorey was much less than elsewhere. In C patchiness of growth was to a large extent correlated with differences in the distribution of the tree species which made up the overstorey.

109 OTHER FACTORS The soil in A was heavier and may have had a greater moisture and nutrient availability, leading to greater growth, than in B or C. From augur samples, the soils in B and C appeared similar, such that differences in growth between these areas were probably not a result of soil factors. Aspect differences appear to have caused the later start to growth in A. Other variables such as slope may also have contributed to the overall differences in growth pattern between the areas.

COMPARISON OF BRAMBLE GROWTH IN WYTHAM WITH

GROWTH AT OTHER SITES

ANNUAL TURNOVER OF BRAMBLE DRY-WEIGHT

110 Above ground biomass in bramble is determined by a number of different processes (Fig. 22^{P,60}). Some estimate of net photosynthetic production i.e. (photosynthesis - respiration losses) is desirable for comparison with other bramble sites and non-bramble species. Because of the other processes in Fig. 20, however, this cannot be calculated from dry-weight data alone. Various ways have been used to obtain a figure for bramble which represents the measurable, annual turnover of dry-weight. These normally involve use of

FIG 21

PROCESSES AFFECTING THE LEVEL OF BRAMBLE BIOMASS

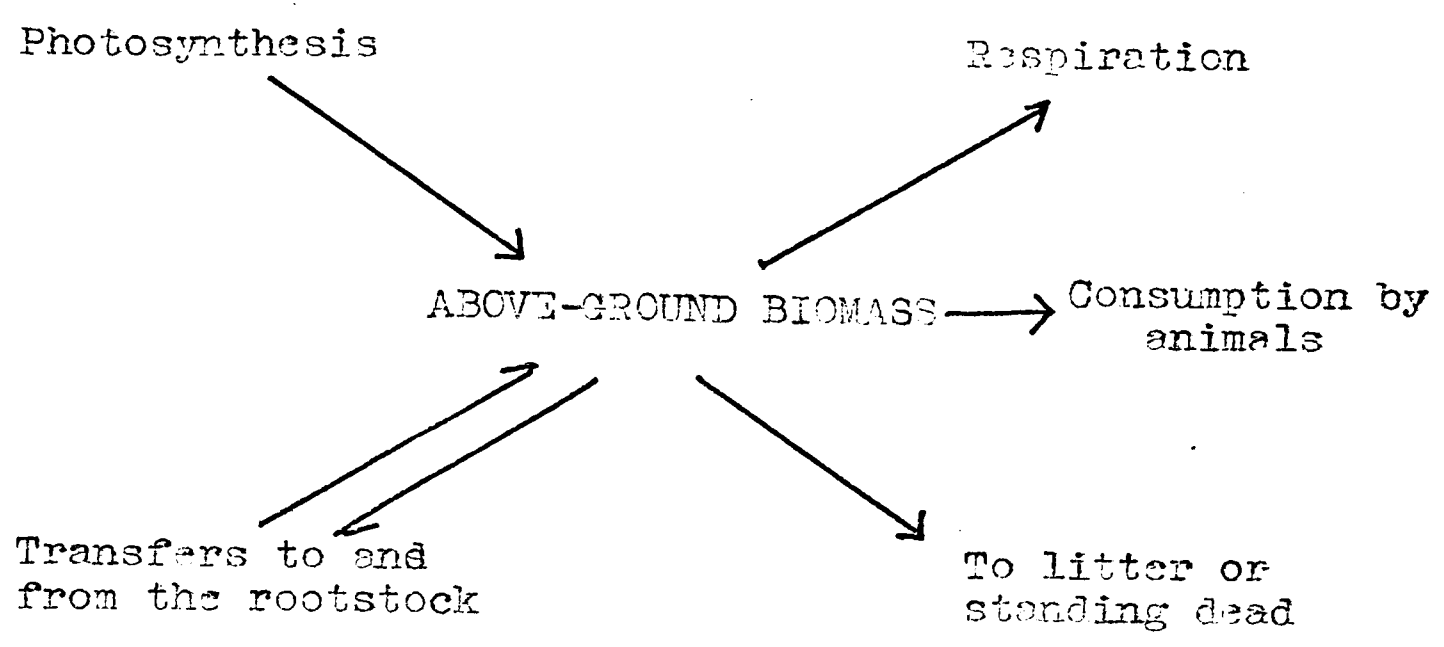


TABLE 16

Author	Site	Soil	Tree cover	Sampling	Comments
Amor (1971)	In Victoria Australia.	Poorly drained, self-mulching topsoil, pH 6.2	None	2 x metre-square plots. Feb. 1969 (mid-summer)	Site representative of growth by <u>R. procerus</u> & <u>R. ulnifolius</u> in that area.
Hughes (1971)	Wynyard wood, Durham, U.K.	Clay or clayey loam on gleyed boulder clay pH 4.5 - 5.5	Mainly alder, birch some sycamore. Under- storey elder, oak hawthorn.	Periodic harvests 1966 - 68. 1967 results used here.	Bramble had the most consistently high biomass, over the two years, of the ground flora.
Hutchings (pers. comm.)	Foxley wood Norfolk, U.K.	Boulder clay	Overgrown hazel coppice, mixed oak- birch canopy.	9m x 9m plot May 1971	Bramble described as dense. Possibly <u>R. dasyphyllus</u> .
Kestemont (1971)	In Vresse district Belgium.	Surface pH 4.9	Oak-birch copsewood Partial understorey of <u>Sorbus sp.</u>	Mid-summer.	Bramble main constituent of ground flora.
Madgwick (1965)	Monks Wood nature reserve U.K.	Poorly drained soil on chalky boulder clay.	Ash coppice. Young elm formed partial understorey.	Three 4m x 4m areas. July 1963	Bramble provided half the ground flora leaf cover.
Sykes & Taylor (In press)	Meathop Wood U.K.	Shallow brown earth. "A" horizon pH 4.1- 7.3	Mixed ash, oak, birch sycamore. Hazel understorey.	Periodic harvests Mar. 1968-Mar. 1969	Bramble (<u>R. vestitus</u>) the most common species over much of the area. Provided 20% of total annual production by ground flora.

DETAILS OF SITES, OTHER THAN WYTHAM, USED IN TABLE 17

TABLE 17

COMPARISION OF BRAMBLE GROWTH
AT DIFFERENT SITES

Column	→	1	2	3	4	5	
Hughes (1971)		34.9	22.2	17.4			g/sq.m.
Sykes & Taylor (In prepn)		65.7	24.6	32.8	40.5	52	..
Madgwick (1965)		82.5		41.2			..
Nestemont (1971)		136		68			..
Wytham C		149	59	74.5	83	107	..
B		277	127	133.5	200	226	..
A		438	175	219	291	295	..
Amor (1971) <u>R. ulmifolius</u>		850		425	570		..
<u>R. procerus</u>		1850		925	1170		..

Column 1 Maximum summer biomass.
" 2 Difference between maximum and March biomass.
" 3 Half the summer biomass.
" 4 Maximum value of (new canes+new laterals+new leaves).
" 5 Maximum weight(new canes+cane leaves)
+ " " (new laterals+lateral leaves).

maximum summer biomass and differ from net photosynthetic production in that no allowance is made for losses by consumption or to the litter layer prior to peak biomass being reached. Transfers to and from the rootstock are also ignored. Different forms of estimate are considered below for the Wytham areas and the sites in Table 16. ^{P.61}

111 MAXIMUM SUMMER BIOMASS As was shown on page 35 the timing and size of peak biomass for bramble depends on three distinct processes of growth and die-back. Peak biomass does not therefore bear any simple relation to annual turnover of dry-weight ^{P.62} (Table 17) .

112 (MAXIMUM - MARCH) BIOMASS This underestimates the annual turnover of dry-weight because some material present in March e.g. most of the third-year cane system dies off before the maximum biomass is reached. Much of the dry-weight in these dying components falls to the litter or enters the standing dead category and is not therefore available to be transferred to new growth.

113 PEAK BIOMASS $\frac{1}{2}$ 2 Over the year as a whole about half the biomass does come from the current year's growth ^{P.49} (Fig. 14). At the time of peak biomass, however, the component's present do not constitute the equivalent of two complete cane systems.

114 SEPARATION OF CURRENT YEAR'S COMPONENTS This seemed to me to be the best way of defining annual turnover of dry-weight for bramble. ^{P.62} Two ways in which it can be done are shown in Table 17 cols. 4 and 5. These differ where the peaks in dry-weight of first and second-year cane systems do not overlap. The main bias in this method, apart from root transfers which are present in the other methods as well, is that material stored in first year canes and subsequently transferred to the laterals appears twice. In this study a decline in dry-weight of canes during lateral growth, indicating

FIG 22

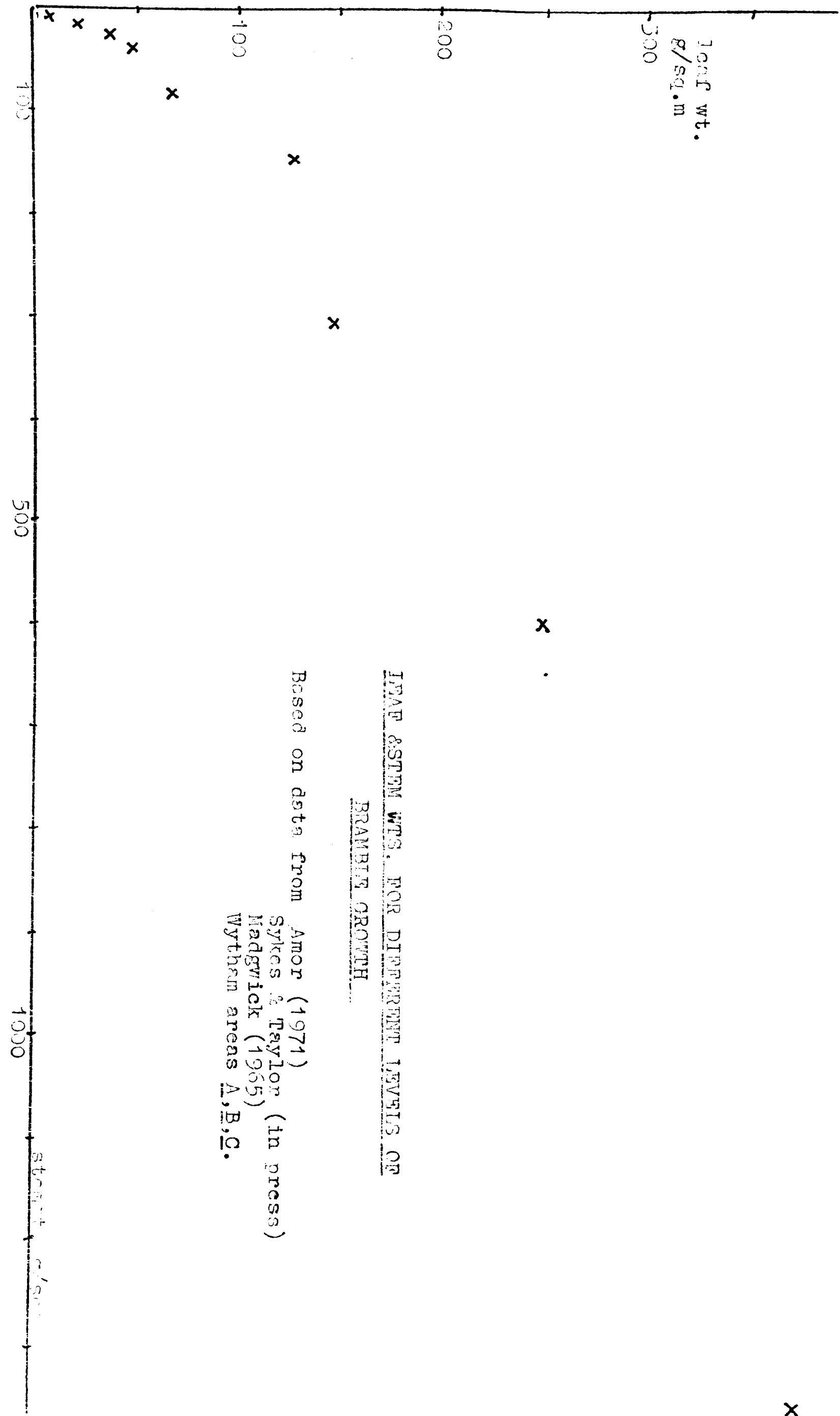


TABLE 18

SUMMER LEAF COVER

Table 18

	Leaf area Index	Leaf wt. g/sq.m
Wytham areas		
C	0.9	67
B	2.1	128
A	2.2	146
Amor (1971)		
<u>R. ulmifolius</u>	2.1	250
<u>R. procerus</u>	3.0	370

TABLE 19

COMPARISION OF DRY WEIGHT DISTRIBUTION
BETWEEN FOXLEY WOOD & WYTHAM

Table 19

	Foxley Wood (Hutchings pers.comm.) May 20 1971	Wytham C Harvest 3 April 1	Harvest 4 May 7 1974	
1st yr. canes (emerging)	1.1	-	3.7	g/sq.m
2nd yr. canes +laterals	30.2	35.0	51.5	"
3rd yr. canes +laterals	28.1	22.7	19.0	"
Leaves	15.0	38.9	47.9	"
Total biomass	74.4	96.6	122.1	"
Dead	61.9	20.9	21.0	"

ing such a transfer, occurred only in area B.

115 HUGHES' METHOD Hughes (1971) estimated annual turnover of dry-weight from inputs to the litter layer. The figure obtained was 89.8 g/sq.m/yr., which is several times the maximum biomass and implies a much faster dry-weight turnover than found in Wytham. This site appears to be exceptional.

116 CONCLUSION ^{P.62} Table 17 suggest that, in woodland with a dense tree canopy or shrub layer, the typical bramble biomass is 50-150g/sq.m., with an annual turnover of dry-weight 50-100g/sq.m/yr. In more open sites such as Wytham A and B, growth may be 3-4 times this. Amor's figures show that potential bramble growth is much greater than that measured here. Even in Britain, bramble growth on open sites can probably be at least twice that found in A.

DISTRIBUTION OF BRAMBLE DRY WEIGHT BETWEEN COMPONENTS

117 LEAF:STEM RATIO Leaf:stem ratio decreased as the mean biomass of the bramble stand increased(^{P.64} Fig. 22) This is found for many plants. Once the canopy is continuous there is an optimum level of leaf cover, beyond which the lower leaves tend to be shaded out. For bramble, this appears to be a leaf-area ^{-index} of about 2-3 as this was found over a wide range of biomass values. Leaf weights showed a greater range(^{P.65} Table 18). The nearly horizontal leaves of bramble result in a low optimum leaf-area-ratio compared to grasses where the leaves are more vertical.

118 FOXLEY WOOD RESULTS Hutchings sampled his bramble stand in May and so the results are not comparable with the other sites, sampled in mid-summer. ^{P.65} Table 19 compares the Foxley wood data with Wytham C for harvests 3 and 4. The distribution of dry-weight between components at Foxley is closer to that for C H3, rather

TABLE 20

Table 20

CONTRIBUTION TO TOTAL DRY WEIGHT PER PLOT
BY THE STANDING DEAD

	Total dry weight	% as standing dead
Amor (1971)		
<u>R. procerus</u>	3460 g/sq.m	46.5
<u>R. ulmifolius</u>	1780 "	52.2
Wytham Areas		
A	593 "	26.1
B	303 "	8.5
C	158 "	6.0
Hutchings (^{pers} comm:)		
Foxley Wood	136 "	45.3

TABLE 21 BIOMASS AND ANNUAL TURNOVER OF DRY WEIGHT
FOR BRAMBLE COMPARED WITH OTHER COMMUNITIES

Table 21

Total ground flora biomass
under various hardwood species 16.2 — 702.2 g/sq.m
(Ovington 1955)

Wytham bramble biomass	<u>A</u>	458	"
	<u>B</u>	277	"
	<u>C</u>	149	"

Annual turnover of dry weight

Grassland	400 - 1300	g/sq.m/yr.	(Gorham &
Bracken	980 - 1410	"	Pearsall
			1956)
Heather	200 - 300	"	(in Gimingham
			1972)
Bramble	<u>A</u>	295	"
	<u>B</u>	226	"
	<u>C</u>	107	"

Above ground material
only

than H4. Growth in Wytham C in 1974 was thus about 6 weeks advanced on Foxley 1971. As a difference of four weeks in the start of growth occurred between two Wytham areas, A and C, in the same year, this is not unreasonable.

119 Leaf weight was less in Foxley than in Wytham. Most of the leaves present at this time were those that had overwintered. At Foxley the main bramble species was probably Rubus dasyphyllus (Hutchings pers. comm.) In Wytham this species showed greater loss of leaves in the autumn than the main species in C, R. vestitus.

120 STANDING DEAD AS% TOTAL DRY WEIGHT From Table ^{P.67} 20 it is clear that the relative amount of standing dead, found in a stand, does not depend on the total weight of bramble present. Hutchings described his stand at "Foxley" as dense, and the stem density was much higher than for Wytham area C, 15 stems/sq.m and 7.2 stems/sq.m respectively. Possibly the greater support and interlacing of stems caused by this high density resulted in dead canes remaining separate from the litter for longer.

COMPARISON OF BRAMBLE STANDS WITH OTHER SPECIES

121 HERB AND SHRUB LAYERS IN WOODLAND Most woodland herbs have annual shoots so that above ground biomass in winter is low. The maximum summer biomass largely represents the annual growth. There is no trend to the variations in above ground biomass between years. With shrubs above-ground biomass tends to increase as individuals age. The annual turnover of dry-weight thus becomes a smaller percentage of total above-ground biomass.

122 Bramble occupies a position between the herb and shrub layers both in size and in growth pattern. There is considerable winter biomass and the standing dead adds to its bulk. The annual dry

weight increase is thus less than the maximum biomass. Unlike shrubs, the level of the winter biomass remains fairly constant. There is little tendency for long term accumulation of material above-ground as occurs in the stems and branches of shrubs.

123 The contribution of other species in the ground layer in A, B and C to undergrowth biomass was not measured. The bramble values alone, however, are comparable to the measurements of Ovington (1955) on the undergrowth found beneath different hard-wood species in plantations (P.67 Table 21). Annual turnover of dry-weight by bramble is similar to that reported elsewhere for herb and shrub layers in woodland.

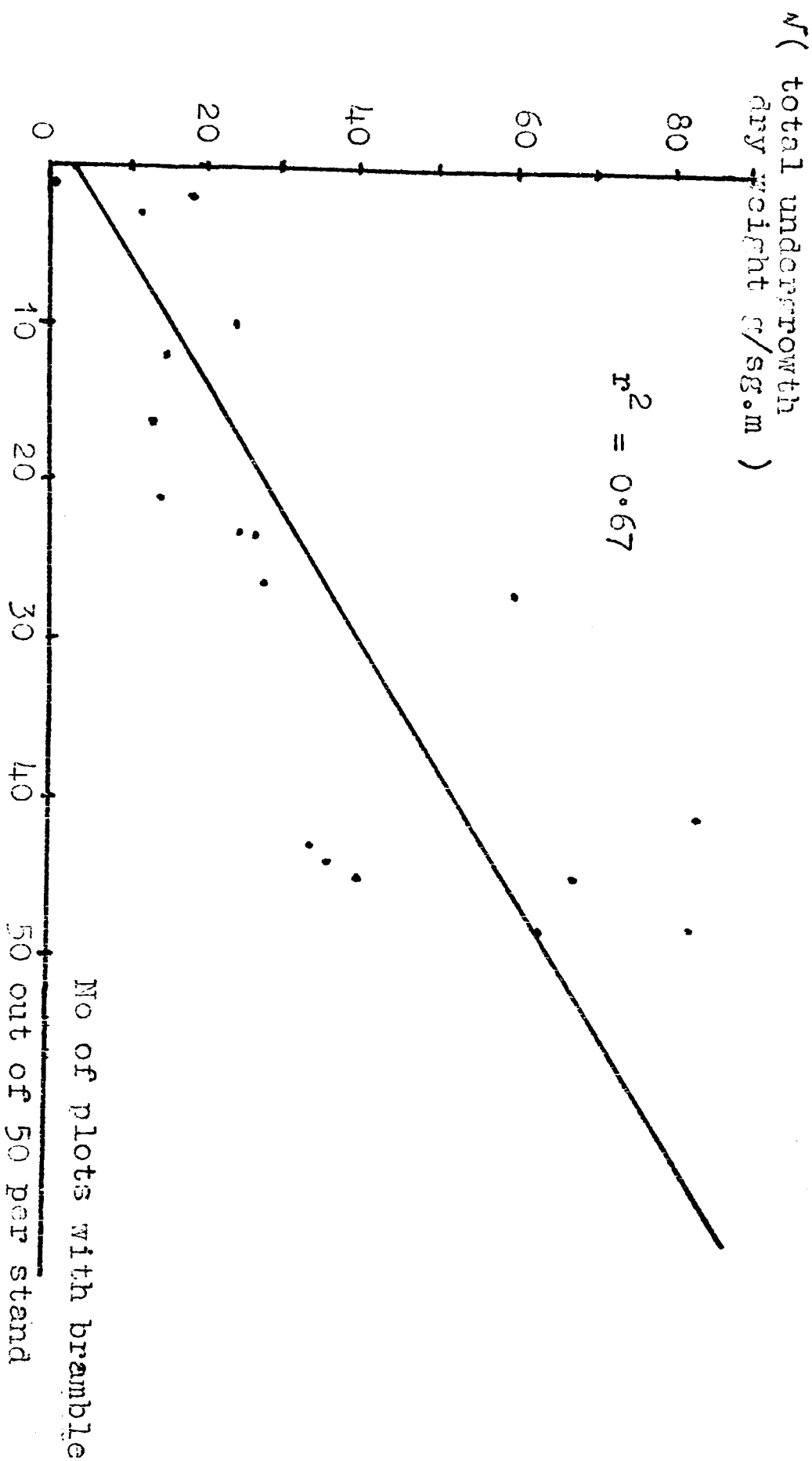
124 OPEN GROWN COMMUNITIES The annual turnover of dry-weight for bramble measured here is low compared to that for various open-grown herb communities, although similar to that for heather, a plant of similar stature. If, as observations suggest, growth of bramble in the open can be at least twice that shown in area A, then bramble is brought ^{into} the range for grassland in Table 21. (P.67)

125 CONCLUSION These results show the important contribution a bramble layer can make to biomass and dry-weight turnover of the ground vegetation in woodland. This is illustrated by the relation between frequency of bramble and undergrowth dry-weight shown in Fig. 23 (P.70) from the results of Ovington (1955). Because the bramble shoot system is relatively short lived cycling of carbon and mineral nutrients is relatively rapid. Bramble has a photosynthetic capacity all the year round because of the winter canopy, but the main growth occurs while the leaves are on the trees. In this it differs from species, such as Endymion non-scriptus, which make their growth during the spring.

FIG. 23

RELATION BETWEEN FREQUENCY OF OCCURRENCE OF BRAMBLE AND TOTAL
UNDERGROWTH DRY WEIGHT FOR VARIOUS HARDWOOD
STANDS

(from results of Ovington 1955)



THE ROOT SYSTEM

126 No full scale sampling of the root system of bramble was carried out in Wytham but a few rootstocks were partially excavated to check for gross differences between the areas. The plants chosen were typical of the areas concerned. As well as Areas A, B and C, roots were looked at in Area D where growth per plant and per unit area were lower even than in C.

127 ROOT CROWNS Crown size decreased from high to low-growth areas. A - D (^{P. 72}Table 22) In D the crown was little more than a slightly swollen region below the base of the stems. In A it was a relatively massive, twisted, knotty object. Amor (1971) reports crown size similar to those in Wytham, 12-40 mm diameter, but Northcroft (1927) found crowns up to 150 mm diameter.

128 MAJOR ROOTS About 4-6 major roots per crown were found in all four areas. Their diameters varied in a similar way to the crown sizes. Spread of roots appeared to be greater in B than in A, but this may be a sampling bias as the sandier soil in B made following the roots much easier than in A. Although Amor (1971) found the bulk of the roots in the top 20cm of soil, in A and B roots were abundant down to 40-50cm depth.

129 CONTRIBUTION TO BIOMASS Amor estimated the contribution of the roots to total biomass as about 40%, Sykes and Taylor (In press) about 50%. From the weights of root extracted from A and B the figures are 24% and 15% respectively of the total summer biomass. As a large and unknown fraction of the root system was not recovered, the true figures were probably nearer the other estimates.

TABLE 22

ROOT SIZES

Table 22

	Area A	B	C	D	
Crown diameters	30-50	20-40	10-30	7-20	mm
Diameters of major roots	7.2 ±1.0	4.8 ±0.3	3.5 ±0.4	2.3 ±0.4	"
Crown weight	36.3 ±13.0	6.7 ±1.8		0.7 ±0.2	g
Total root wt. extracted	43.9	13.4		2.2	g/rootstock
Spread from rootstock	60	80	40	30	cm

Based on partial excavation of six rootstocks per area.

130 Differences in above-ground growth appeared to be matched by below ground differences. The large size of some of the crowns suggests that they may act as storage organs to supply the early growth of first-year canes. Differences in the mean age of rootstock may contribute to the differences in root size between areas. Two of the rootstocks examined in D had been formed recently from tip-rooted stems. Turnover of plants may be higher in this area because it is a marginal site for bramble growth.

REPRODUCTION IN BRAMBLE

FLORAL REPRODUCTION

INTRODUCTION

131. There has been little work done on flower and fruit production in "wild" bramble populations, although extensive work has been done with raspberries and some blackberry cultivars. Observations were made of flower and fruit abundance in the different areas studied in Wytham.

132. The main period of flowering was from the end of June to the beginning of August. Flowers were found at other times of the year although these did not fruit. The bulk of the flowers were borne on second-year canes but with some on third-year canes also.

FLOWER INITIATION AND DEVELOPMENT

133. PRIMORDIA INITIATION The flower primordia are laid down in the buds in early spring in wild brambles (Robertson 1957) although in raspberries and blackberry cultivars the primordia are formed in the previous autumn. In raspberry, initiation and subsequent floral development are encouraged by shortening days accompanied by low temperatures (Williams 1960). Bramble may have a similar requirement because any laterals formed in the first year remain vegetative.

134. BUD DEVELOPMENT Up to three buds are present at any node, of which only the primary normally forms a lateral. (Robertson 1957). The

other buds are less well-developed, but are capable of growing out if the primary bud is damaged or forms a lateral in the first year.

135. Gradients of bud development occur along the cane. In raspberry, bud differentiation begins at the cane tip and proceeds to the base. In blackberry those in the middle of the cane develop first and produce the largest inflorescences (Robertson 1957). It is from the basal zone that laterals formed in the second year, which remain vegetative, develop. (Heslop-Harrison 1959).

INFLORESCENCE NO's PER UNIT AREA IN WYTHAM

136. ^{P.76} DEATH BETWEEN FLOWERING AND FRUITING Table 23. Inflorescences that fail to bear any fruit die and there may be further deaths at the young fruit stage. As a result the mean number of live inflorescences per unit area declined in B and C from July to September. In A nearly all inflorescences bore some fruit, though not every flower on an inflorescence. The decline in live inflorescence numbers did not occur, therefore, until September when the fruit was ripe.

137. 1974/1975 COMPARISON Inflorescence numbers were lower in 1975 than in 1974 for B and C. Flower and fruit production may have been less in 1975, or, since there was only one observation time in 1975, flowering may have been more advanced and more inflorescence death have occurred.

138. Flowering was clearly greatest in areas of most vigorous growth. In the regrowth of bramble, which had been cut back in part of B, flowering was less than in the uncleared bramble. No live inflorescences

TABLE 23

LIVE INFLORESCENCES
PER UNIT AREA

1974	28th July	14th Aug.	4th Sept.	19th Sept.	
Area					
A	21 ±1.1	20.9 ±1.5	18.6 ±2.2	13.9 ±1.8	per sq.m.
B	16.2 ±2.3	11.5 ±1.3	2.6 ±0.7	3.2 ±1.0	"
C	8.6 ±3.1	5.0 ±1.4	0.2	0.1	"
1975		10th Aug.			
A		22.8 ±1.6			"
B		5.2 ±1.3			"
C		1.2 ±0.5			"

Figures for Aug. 14th, Sept. 19th, 1974 are mean inflorescence number for 10 plots per area. Figures for other dates are based on 5 plots per area.

TABLE 24

FLOWERING ON INDIVIDUAL
CANES

Table 24

Area	A		B		C	D	
Year	1974	1975	1974	1975	1974	1975	
Laterals per cane	16.0 ±2.7	18.2 ±1.6	9.8 ±0.7	10.8 ±1.0	7.4 ±1.2	5.1 ±0.6	
Nodes not bearing a lateral	32.8	17.0	32.9	32.3	31.5	20.4	%
Laterals which bore flowers.	79	77	35	68	33	0	%
Laterals which bore fruit	68	61	9.6	4.5	3	0	%
Laterals flowering but not fruiting	14	18	72	91	90	-	%
... ..	13		84		98	% from no.s of inflorescences per unit area.	

Based on 5 canes per area.

were found in 3 regrowth plots on August 10, 1975, compared to a mean of 5.2 for control plots.

FLOWERING AND FRUITING ON INDIVIDUAL CANES

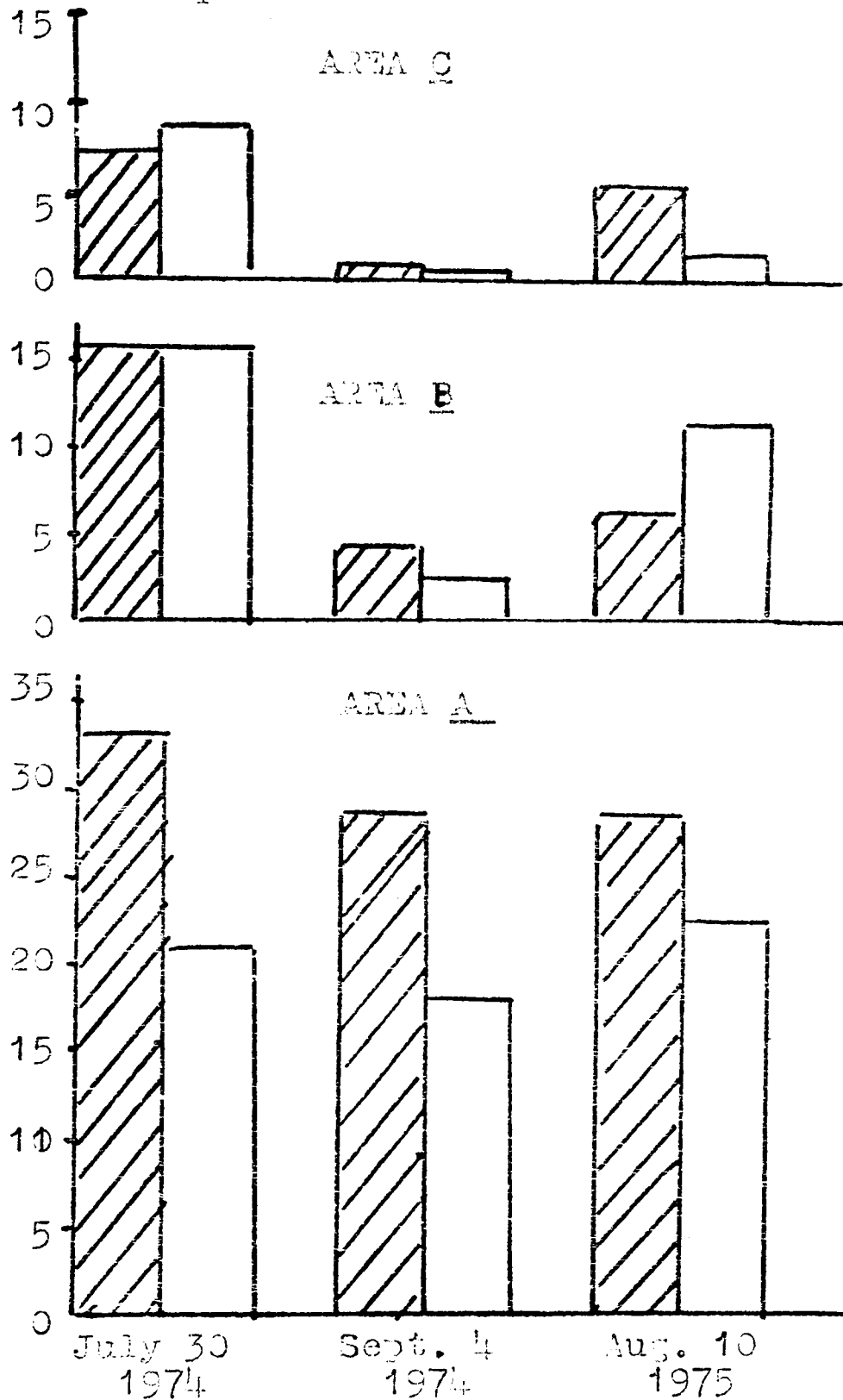
139. PERCENTAGE OF BUDS DEVELOPING Robertson (1957) found that 34 - 48% of nodes on raspberry canes failed to produce laterals. For bramble in the different areas about 30% of nodes failed, mainly in the tip and basal zones of the cane (^{P. 76} Table 24). Towards the tip the buds appeared to be alive, but were small and undeveloped. Many of the buds in the basal region died. The moister microclimate may have led to greater attack by micro-organisms in this region compared to the rest of the cane.

140. PERCENTAGE OF LATERALS BEARING FLOWERS AND FRUIT ^{P. 76} Table 24 gives the percentage of laterals which bore flowers and fruit in the different areas. As with the unit area values, flowering success declined from A - C. The percentage of laterals that flowered in B in 1975 was nearly twice that in 1974. This was thought to be associated with the more vigorous lateral growth shown by the 1975 sample-mean lateral length 35 cm, compared to 28 cm in 1974. This suggests that the lower inflorescence number per unit area measured in B, 1975 (^{P. 76} Table 23) was a result of more advanced flowering, rather than less flowering.

141. ESTIMATED INFLORESCENCE NO's /sq. M The data from the individual cane measurements and cane density were used to calculate expected numbers of inflorescences per metre - square (^{P. 78} Figure 24). The estimates for area A are all much higher than the observed, possibly

OBSERVED AND EXPECTED INFLORESCENCE NOS
PER METRE-SQUARE PLOT

Inflorescence nos
per metre-square



= expected no. Mean inflor. no/cane X canes/sq.m

= observed no.

because the denseness of growth meant that some inflorescences were not counted.

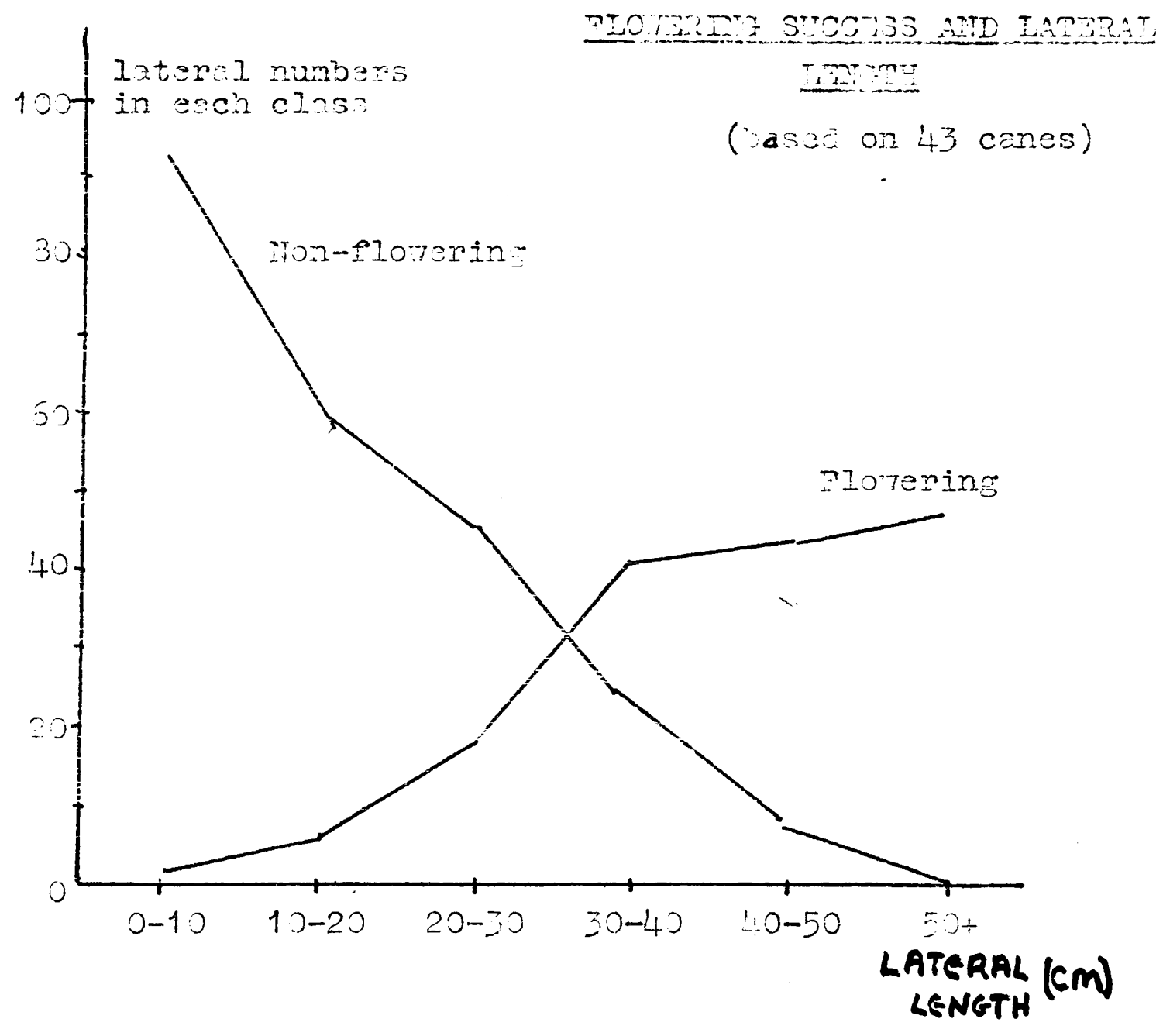
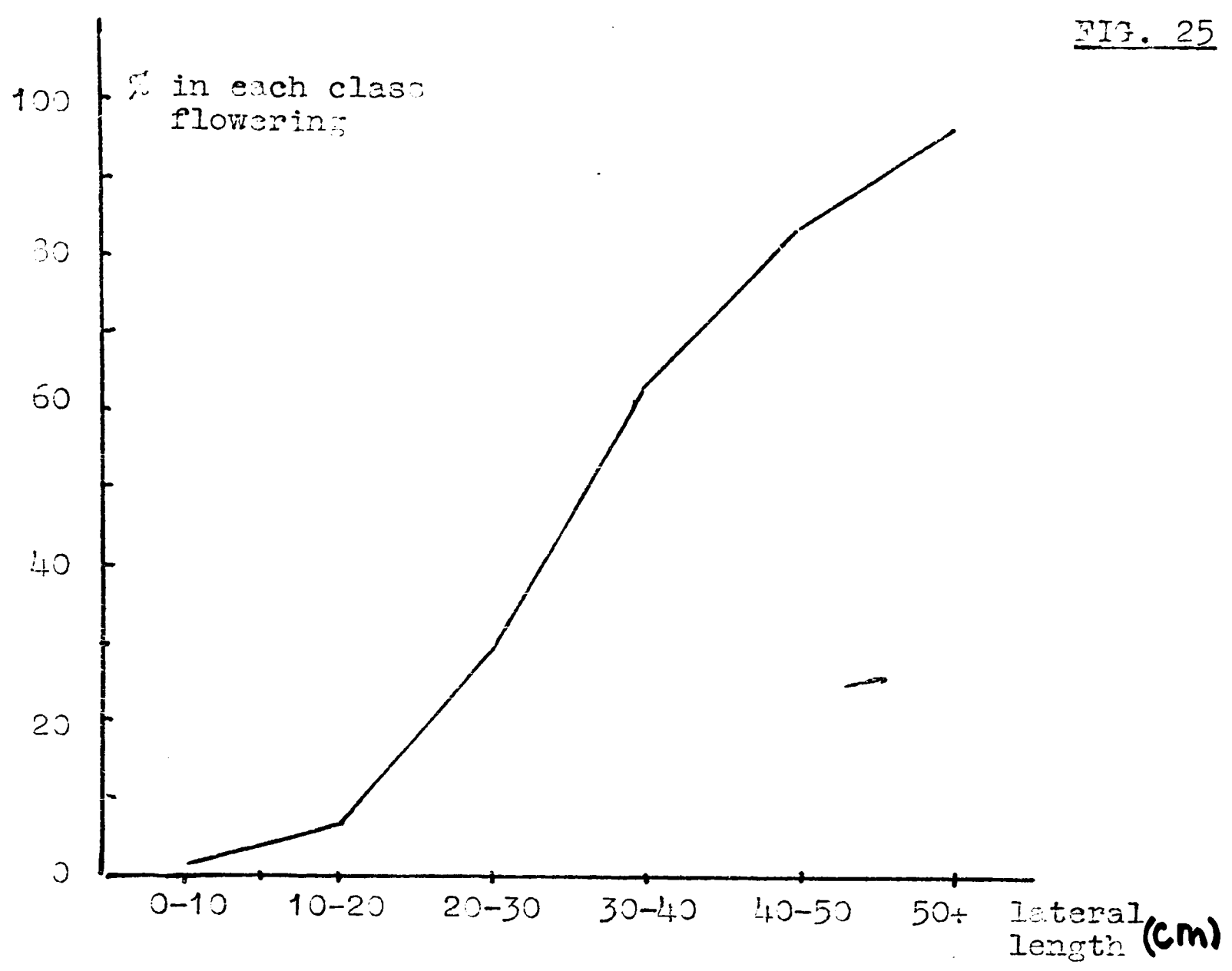
CAUSES OF FLOWERING DIFFERENCES BETWEEN AREAS

142. DEGREES OF SHADE Increased flowering under higher light intensity is found for many species. A had the least dense shade and the most flowering by bramble, D the densest shade and the least flowering. A, however, also had most vigorous bramble growth, D the least.

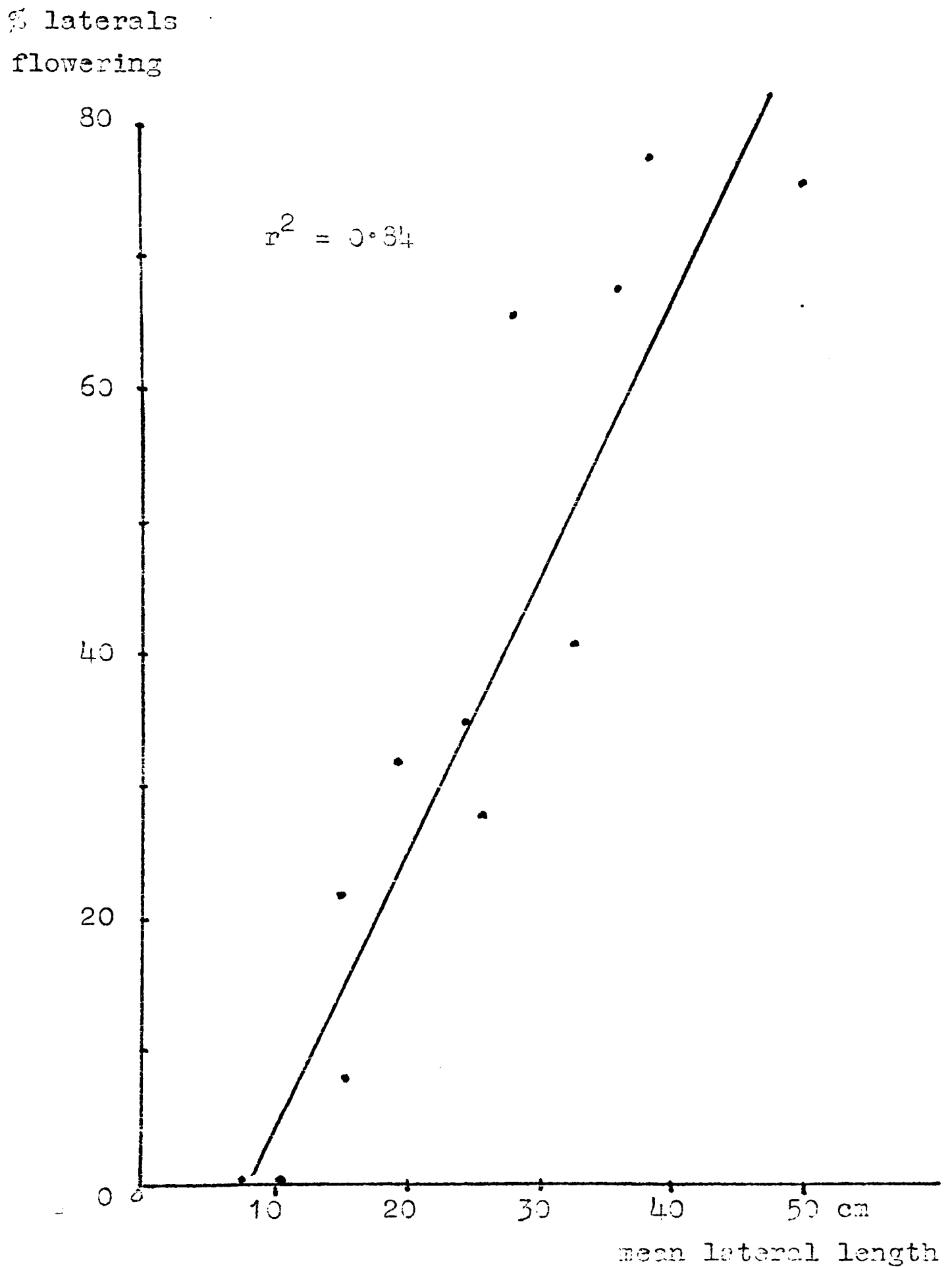
143. CORRELATION BETWEEN FLOWERING AND LATERAL VIGOUR ^{P.80} Figure 25 shows the relation between flowering and lateral length. The longer the lateral, the greater the chance that it would bear an inflorescence. The same relation is shown in a different way in Figure ^{P.81} 26. This relationship could be partly caused by flowering and lateral growth both responding to the same environmental factor: high light perhaps increasing growth, but also flowering. However within an area reduction of the vigour of canes eg. by defoliation or in the regrowth, also caused a reduction in flowering. Thus a direct link between flowering and vigour existed.

144. Lateral vigour was linked to cane growth, the longest laterals being found on the strongest growing canes, and flowering was similarly greatest on the most vigorous canes. A similar correlation was found for raspberries, between berry yield per lateral and cane diameter. (Crandall et al. 1974a).

145. Lateral vigour was also related to its position on the cane. There was a tendency for lateral lengths to decline along the cane ^{P.82} (Figure 27). Laterals formed on side branches were smaller than those on the

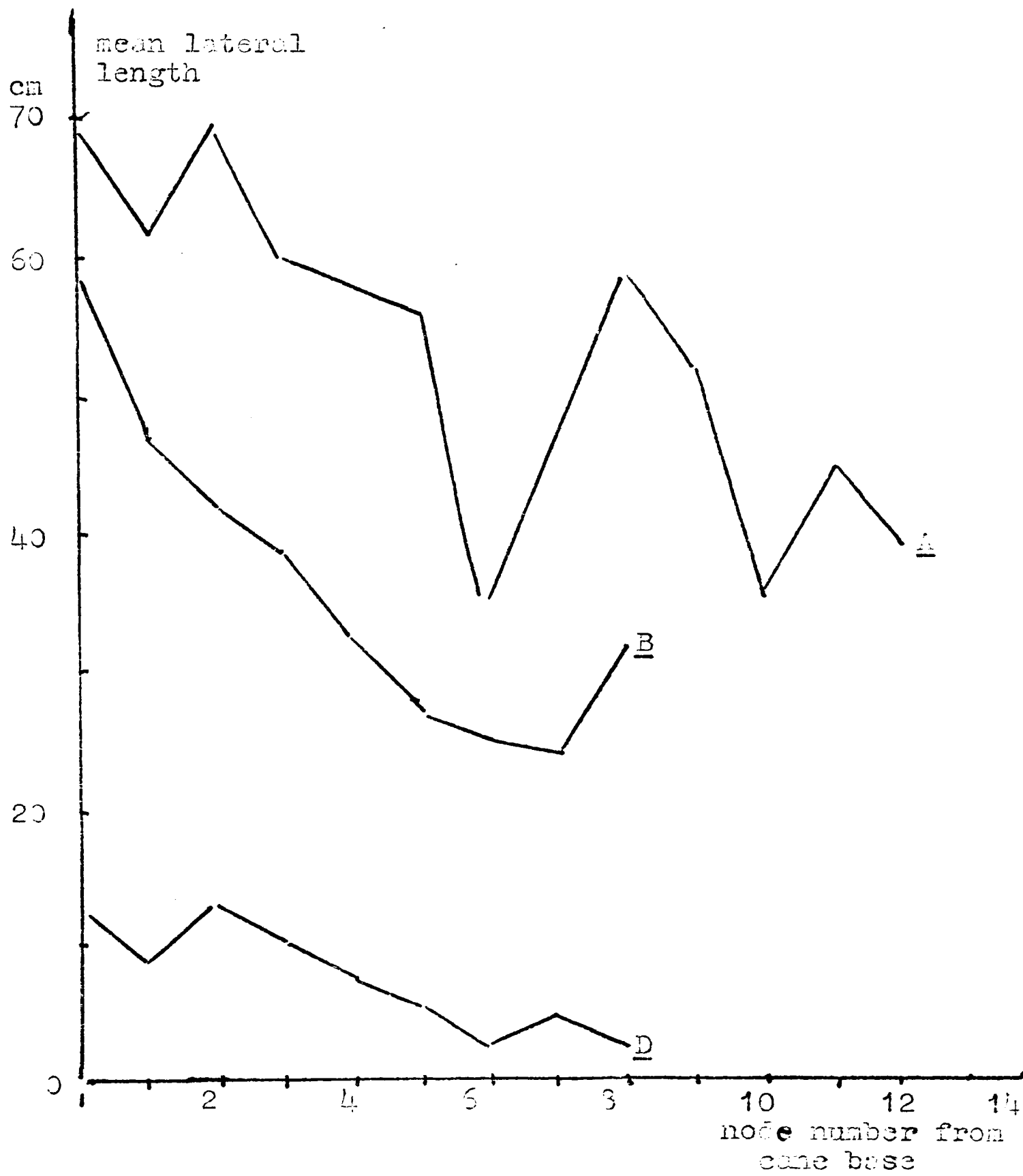


MEAN LATERAL LENGTH & % FLOWERING
FOR DIFFERENT GROUPS OF CANES



The points show the mean lateral length and % laterals flowering for different groups of canes, measured in areas A, B, C, D, in 1974 & 1975. Regrowth and defoliated canes are included.

FIG. 27



The lines are based on 5 canes per area.

LATERAL LENGTH AND POSITION ON CANE

main stem at nodes adjacent to the one at which the side branch originated.

DISCUSSION

146. The correlation between lateral length growth and flowering probably results from both depending in part on cane reserves. Large diameter canes in raspberries were found to have greater amounts of stored carbohydrate per bud than smaller canes. (Crandall et al. 1974 b.). The amounts of stored carbohydrate per bud might be expected to decline along the cane as its diameter decreases. Side branches which have smaller-diameters than the main stem would similarly have smaller reserves. In blackcurrants floral development and fruit formation are markedly affected by the vigour of adjacent internodes and leaves (Rudloff 1960). This association between vigour and flowering success contrasted with the results for vegetative reproduction, which was most prominent in areas of weak bramble growth.

TIP-ROOTING BY CANES

INTRODUCTION

147. Tip-rooting of canes was the main means of vegetative spread in Wytham. Growth of suckers from exposed roots was not common. Tip-rooting by bramble stems was recorded in classical times by Theophrastus. Heslop-Harrison (1959) described the process in detail for Rubus ulmifolius and the main points in the process are given below.

148. DESCRIPTION OF TIP-ROOTING In autumn there is a change in the nature of the stem apex, such that it starts to grow downward until it

contacts the ground. The stem becomes thinner than normal growth and is juvenile in structure. The leaves along it are progressively less well-developed. At some time after it reaches the ground the stem apex swells and internode expansion is reduced. Roots grow out from this swollen "boss." The apex turns upward and forms a resting bud which the following spring develops into a new cane. Die-back of the parent cane in the following autumn separates the daughter plant from the parent rootstock.

149. STEMS SHOWING TIP-ROOTING In Wytham tip-rooting was largely confined to first-year canes and laterals produced in the first year, often as a result of damage to the cane apex. Heslop-Harrison (1959) found tip-rooting by vegetative laterals formed on second-year canes. Such laterals, however, were not common in Wytham.

150. LIGHT REGIME AND ROOT BOSS FORMATION During the period in which tip-rooting occurs in the field, day-length is shortening. Root-boss formation is stimulated by placing the cane apex under reduced light conditions (Barnola 1971). The same effect was achieved more rapidly by covering the tip in a light-proof bag for two weeks (Heslop-Harrison 1959).

151. VIGOUR OF GROWTH AND TIP-ROOTING Barnola also concluded that treatments which restricted the growth of a cane tended to lead to tip-rooting by that cane. Canes that were growing strongly were less likely to root than weak canes. He also found that cane apices pointing downwards were more likely to respond to treatments designed to increase tip-rooting than upward-pointing ones.

STEM-APEX COVERING AND ROOT-BOSS FORMATION IN WYTHAM

152. **METHODS** On July 21, 1975, fifteen canes in area A had the last two expanded internodes covered by black, light-proof fabric bags. A similar number had their tips covered by clear, polythene bags, with a third group marked as controls. This was repeated in areas B and D. Five bags of each sort were removed after 2, 3 and 6 weeks respectively in each area. Further sets of canes were "bagged" on August 12th and September 9th and the bags left on for 3 weeks. The results are shown in Tables ^{P.86} 25 and ^{P.87} 26.

153. **APPEARANCE AND GROWTH OF CANES** Growth of "bagged" canes was significantly less than that of the controls although there was no difference between fabric and polythene bags in this respect. In areas A and B covering the tip for more than 14 days greatly reduced growth, but in D the duration of "bagging" made little difference to the reduction in growth caused. While the fabric bags were on, new growth was white, but it rapidly became green once the bags were removed.

154. **ROOT BOSS FORMATION IN A AND B** Some of the canes inside the polythene bags showed swelling of the stem apex, but neither these nor the controls produced root bosses. Root bosses were formed inside the fabric bags but only if these were left on for 21 days, compared to 14 days in Heslop-Harrison's experiments.

155. **ROOT BOSS FORMATION IN D** Almost all the canes in D tip-rooted. Those inside the fabric bags produced root bosses while the tip was still covered, earlier than for the other treatments. Controls and those inside polythene bags only rooted after contact with the ground.

156. **STABILITY OF INDUCED ROOT BOSSES** Cane growth continued beyond the root boss with nine of those formed inside fabric bags in D and two

TABLE 25

EFFECT OF "BAGGING" CANE APICES
ON SUBSEQUENT LENGTH GROWTH

Table 25

a) Increase in cane length, 21st July - Oct. 3rd.

	Area	A	B	D	
Tip-covering					
Fabric bags		27.2	24.8	25.9	cm
Polythene bags		30.4	4.6	32.9	"
Controls		48.7	28.0	52.5	"

Based on 15 canes per treatment.

Analysis of variance.

	df.	variance ratio	
Area	2	13.6	***
Tip-covering	2	11.1	***
Interaction	4	1.5	
Residual	126	R.M.S. 501	

b) Duration of "bagging" and length growth, 21st July - Oct. 3rd.

	Area	A		B		D	
Bags	Poly- thene	Fabric	Poly- thene	Fabric	Poly- thene	Fabric	
Duration of bagging							
14 Days	49.4	40.0	10.0	38.0	39.4	30.1	cm
21 "	25.2	23.0	1.1	8.0	46.5	27.5	"
42 "	16.6	18.6	2.7	1.4	22.6	30.2	"

Based on 5 canes per treatment.

Analysis of variance.

	df.	variance ratio	
Polythene/fabric	1	0.6	
Area	2	15.2	***
Duration of bagging	2	5.3	**
Duration x Area	2	3.5	*
Residual	72	R.M.S. 283	

The remaining interactions were non-significant.

TABLE 26

ROOT BOSS FORMATION

Table 26

a) Total numbers of root bosses formed.

	Area	A	B	D	
Tip-covering					
Controls		0	0	11	15 canes/area
Polythene bags		0	0	13	} 35 canes in A & B each 20 " " D
Fabric bags		9	4	14	

b) Duration of bagging and root boss formation.

	Area	A	B	D	
Duration of bagging.		Fabric	Fabric	Fabric	Poly-thene
Bagged July 21st					
14days		0	0	4	4 5 canes
21 "		0	0	2	4 per treatment
42 "		5	1	5	4 "
Bagged Aug. 12th					
21days		2	1	3	1 10 canes each A & B. 5/treatment in D.
Bagged Sept. 9th					
21days		2	2	-	- 10canes each A & B.
No canes were bagged in <u>D</u> on Sept. 9th as by this time boss formation on the controls was well advanced.					

TABLE 27

TIP-ROOTING BY DEFOLIATED CANES

Table 27

Areas A & B. There was no tip-rooting by either control or defoliated canes.

Area <u>D</u>	Defoliated	Control	
Canes tip-rooting	1	6	Probability =0.0195 (Fisher exact test)
Not " "	7	2	

from A. The section of stem beyond the boss was of the juvenile, rooting type and in some cases a second boss was formed after the apex had reached the ground. In these canes the induction of the change in the stem apex was not complete.

157. ROOT GROWTH No roots grew out while the bosses were still in the bag. Where a boss did subsequently contact the ground, the tubercles on the lower side only developed into roots. Heslop-Harrison suggests that the low humidity in the bags may be responsible for the roots not developing.

158. DISCUSSION These results confirm those of Barnola and Heslop-Harrison that absence of light is an important factor in root boss formation. My results are less clear-cut than in the other experiments, where all the treated canes formed bosses. Greater variation was introduced in the Wytham experiments by the use of non-clonal material, under field rather than laboratory conditions.

159. Area D, which had the least vigorous canes, showed the greatest response in terms of root boss formation. A which had the most vigorous growth was expected to show less of a response than B. The reverse, however, occurred. Cane growth was beginning to decline at the beginning of the experiment particularly in B. If only actively growing cane apices can show the response then the lesser response of canes in B than A may have been because some of the canes in the former had virtually ceased growth.

160. During normal tip-rooting the cane may grow some way along the ground before roots are actually produced. Often some covering of the stem apex occurs naturally, as it grows into a soil crack or under litter,

and this may induce root production.

DEFOLIATION OF CANES AND TIP-ROOTING

161. **METHOD** Eight first-year canes in A and D, and fifteen in B had their leaves removed as they formed. The canes were checked for new leaves at least once a week. A similar number were marked as controls. The numbers in each treatment that tip-rooted the following autumn are shown in Table 27.
P. 87

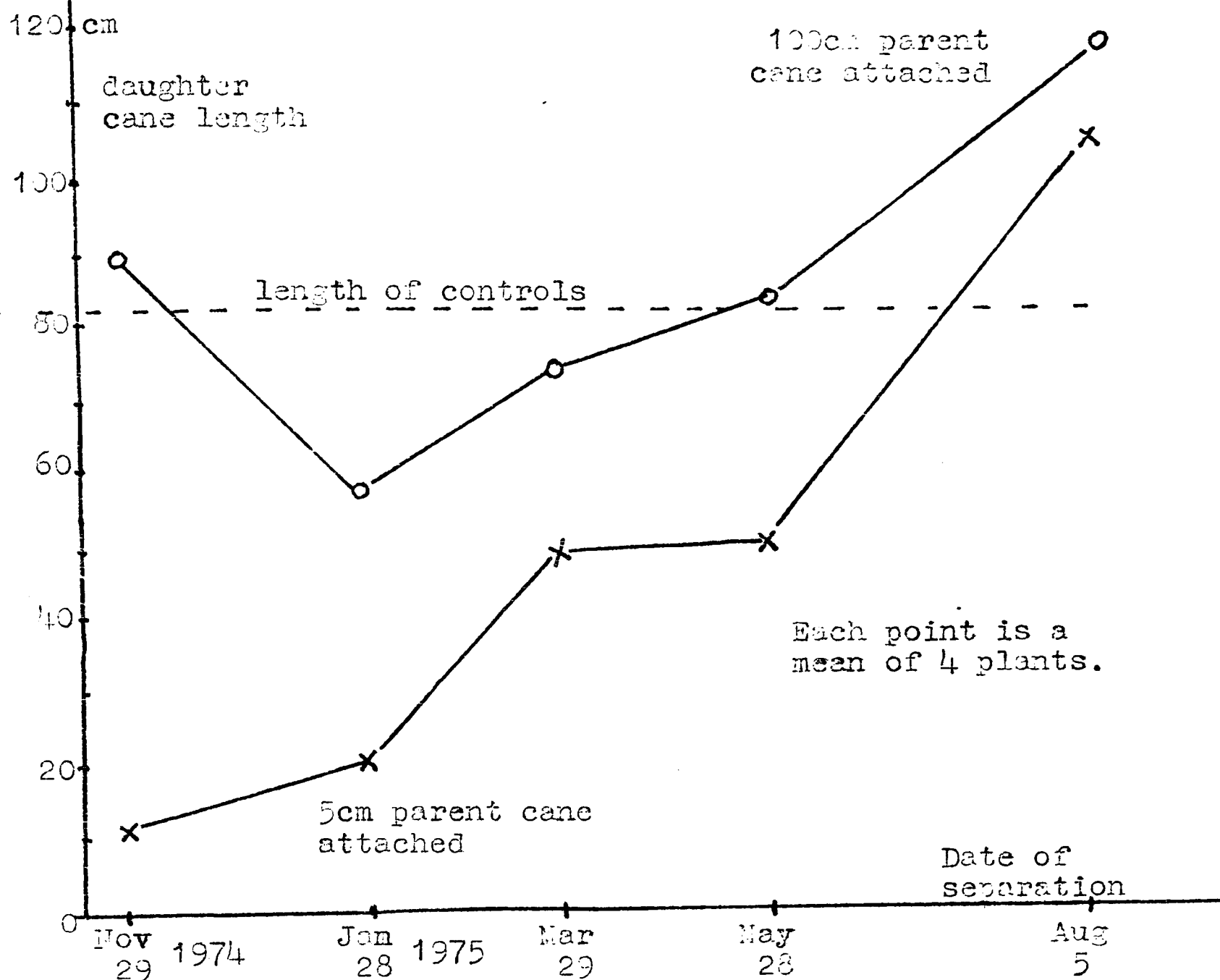
162. **DISCUSSION** Defoliation by reducing the vigour of the canes was expected to increase tip-rooting. The converse happened. The removal of the leaves from the canes in D made them more upright, because there was not the leaf weight to bend the canes over. Barnola showed that upright canes were less likely to tip root than downward pointing ones, which may be the reason that there was less tip-rooting by defoliated canes.

GROWTH OF DAUGHTER PLANTS

163. The relations between the daughter plant formed from a tip-rooted stem, the parent cane and the laterals produced on the parent cane were investigated. The daughter plant was separated from the parent cane at different intervals after the initial rooting of the apex and with different lengths of parent cane left attached to the plant.

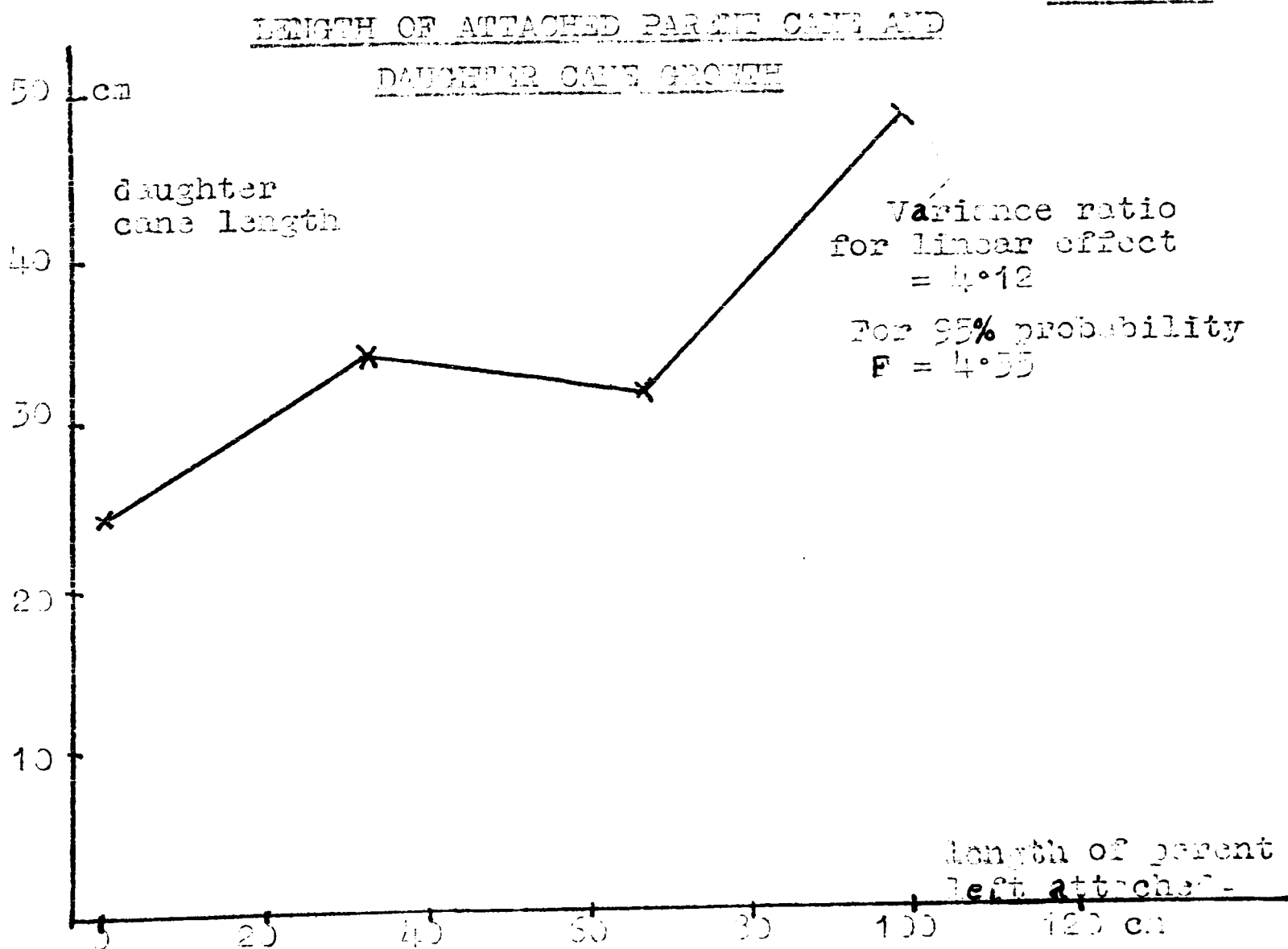
EFFECT OF TIME OF SEPARATION ON GROWTH OF DAUGHTER PLANTS

164. In autumn 1974 a number of tip-rooted canes were marked in part of area B. At roughly two monthly intervals during the following year



DATE OF SEPARATION AND DAUGHTER CANE GROWTH

FIG. 29



eight daughter plants were selected at random from those marked and the parent cane cut. At each date, for four of the plants the parent cane was cut at about 5 cm from the daughter plant, while for the other four 100 cm of parent cane with from 8-10 leaves was left attached to the daughter plant. The length of the new cane produced by the daughter plant was followed during 1975.

165. ^{P. 90} RESULTS Figure 28. There was no significant difference in growth of daughter plants between the controls, left attached to their parent rootstock and those separated, but with 100 cm of parent cane left attached. New cane growth was 60-70% that of canes on established rootstocks. The leaves on the parent cane section stayed alive.

166. 5 cm PARENT CANE LEFT ATTACHED The time at which the daughter plant was severed from its parent was important where only a short length of parent cane was left attached. Two of the plants separated on November 19th died, as did one from January 23rd. Growth of the new cane increased the longer the interval between the initial rooting and the separation from the parent plant. By the beginning of August cutting the parent cane had no further effect on daughter cane growth.

CRITICAL LENGTH OF PARENT CANE, GROWTH OF LATERALS ON DETACHED PARENT CANES

167. In autumn 1975, forty-eight tip-rooted canes in D were marked ^{P. 92} and assigned at random to the treatments in Table 28. The experiment aimed to determine the minimum length of cane that had to be left attached to a daughter plant for subsequent cane growth to be normal. A second aim was to discover whether the daughter rootstock could support full lateral growth on the parent cane if the latter were separated from its own

TABLE 28 LENGTH OF ATTACHED PARENT CANE AND GROWTH
OF THE DAUGHTER PLANTS

Table 28

Length of parent cane left attached to the daughter plant.							
	<u>Controls</u>	<u>+full</u> <u>cane</u>	<u>+100cm</u>	<u>+66cm</u>	<u>+34cm</u>	<u>+0cm</u>	
Parent cane cut							
on Nov.26th 1975	56	80	46	0	34	0	Daughter cane lengths (cm)
	58	100	33	17	35	17	
	120	68	72	67	20	13	
on Mar.15th 1976	45	56	45	29	13	28	"
	44	73	60	32	51	13	
	42	71	36	17	26	20	
	55	85	51	16	60	78	

+full cane - the parent cane was cut as close to the parent rootstock as possible.

+0cm - the parent cane was cut as close to the daughter plant as possible.

TABLE 29 LATERAL GROWTH ON CANES SEPARATED FROM EITHER Table 29
PARENT OR DAUGHTER ROOTSTOCKS.

	Controls	+full cane	+0cm	
Parent cane cut on				
Nov.26th	7.4	7.3	14.0	Mean lateral lengths per cane
	11.6	5.0	7.3	
	12.3	2.0	20.5	
Mar.15th	4.0	4.8	9.1	"
	11.5	10.4	15.0	
	4.9	4.6	9.5	

Analysis of Variance		
	df.	variance ratio
Time of separation	1	0.64
Point "	2	4.5
Interaction	2	1.6
Residual	12	R.M.S. 16

rootstock.

168. RESULTS: NEW CANE GROWTH Variability was much higher than in the previous experiment, in B, and one replicate of the November separation was destroyed by deer. As a result no significant difference was detected between the two times of cutting the parent cane. For analysis of the effect of length of parent cane left attached the treatments were grouped in two ways.

(1) CONTROLS, + FULL CANE, + 100 cm. There was no significant difference between these three treatments. This confirms the result of the previous experiment that about a metre of parent cane left attached ensured normal growth of the daughter plant.

(2) + 100 cm, + 66 cm, + 34 cm, + 0 cm. Analysis of this group showed a strong tendency for the length of the new cane to increase with the length of parent cane left attached. Figure 29. The F ratio for the linear trend was only slightly below that for the 95% probability level.

169. LATERAL GROWTH ^{P. 92} Table 29. The laterals on the control parent canes were compared with those on the "+ FULL", where the cane was cut at the parent rootstock end, and "+ 0" where the cane was cut at the daughter rootstock end. There was no difference in the number of laterals produced in the three treatments. Length growth of laterals was, however, significantly different, although the differences in length were not great. The daughter plant was not quite as effective as the parent rootstock in supplying the needs of the developing laterals. The greater growth of laterals when separated from the daughter plant suggests possible competition between the two.

TABLE 30

EFFECT OF DEFOLIATION ON
DAUGHTER CANE GROWTH

Table 30

	Controls	Laterals on parent cane defoliated.	New cane only defoliated	New cane & laterals defoliated	
Daughter attached to parent cane	37 48 47 52	50 28 36 38	35 34 22 49	11 37 22 23	Lengths of new canes (cm)
Daughter separated from parent cane	16 31 15 21	26 16 17 19	0 0 3 0	0 5 6 7	"

Analysis of Variance

	df.	variance ratio	
--	-----	----------------	--

Separation from parent cane	1	83.4	***
New cane defoliation	1	33.2	***
Lateral defoliation x separation	1	4.5	*
Residual	24	R.M.S. 55.5	

Other main effects and interactions were non-significant.

TABLE 31

LATERAL GROWTH AND THE DEFOLIATION
OF DAUGHTER CANES

Table 31

	Controls	Laterals on parent cane defoliated.	New cane only defoliated	New cane & laterals defoliated	
Daughter attached to parent cane	14.8 23.6 11.3 19.3	8.1 3.8 6.0 6.2	14.1 12.0 14.7 8.8	6.0 4.5 6.5 3.0	Mean Lengths of laterals per cane (cm)
Daughter separated from parent cane	17.5 14.0 22.5 17.3	8.2 6.2 3.0 4.5	11.4 17.0 16.9 23.1	2.5 6.8 2.8 1.4	"

The reduction in lateral length caused by lateral defoliation is significant, all other main effects and interactions are not.

COMBINATION OF DEFOLIATION AND SEPARATION TREATMENTS ON NEW CANE GROWTH

170. The effect of defoliation of the new cane was investigated with reference to its dependence on the parent cane and competition with lateral growth. Tip-rooted canes in B were assigned to the treatments in Table ^{P.94} 30. New leaves were removed as they formed, where appropriate, at weekly intervals.

171. RESULTS Lengths of laterals and of the new canes are shown in ^{P.94 and 31} Tables 30/ for the different treatments. Growth of the laterals was not affected by the presence of or the treatment of the new cane. Growth of the new cane was, however, reduced by defoliation of the laterals. This could imply that either the laterals contribute to growth of the new cane or that both compete for the same cane reserves. The latter seems more likely and defoliation of the laterals then increases their drain on these reserves.

DISCUSSION

172. TIME OF DAUGHTER PLANT INDEPENDENCE The parent cane starts to die-back about a year after it tip-roots. By this time, therefore, the daughter plant must be independent of the parent cane and rootstock. Amor (1974 b) found no difference in the response of daughter plants to herbicides or mowing, between those still attached to and those separate from the parent plant, at 11 months old. My results suggest that the daughter plant may become effectively independent of the parent by the end of July - or about 9 months old.

173. TRANSFER FROM PARENT TO DAUGHTER PLANT The main source of material transferred to the daughter during its growth is the cane and its

leaves, not the parent rootstock, and in particular the section of cane closest to the daughter. The transfer starts in the autumn as soon as the tip has rooted. Over the winter, although there is no new stem growth, considerable root growth occurs. Root lengths increased from 6-10 cm in November to more than 40 cm by the beginning of March. Transfer to the daughter plant continues through the spring and early summer.

174, MOVEMENT FROM DAUGHTER TO PARENT CANE Amor (1974 a) noted that die-back of tip-rooted stems started in the middle and progressed towards both ends, whereas ordinarily canes died back from the tip. Lees (1884) found that a tip-rooted stem severed from its original rootstock remained alive for a year. This indicates that movement of material from daughter plant to parent cane can occur. My experiments showed that not only can the parent cane survive, when attached only to the daughter rootstock, but lateral growth on that cane is not greatly reduced. The normal direction of movement in the parent cane conducting tissues is reversed in this situation.

175. DAUGHTER CANES AND LATERAL GROWTH The daughter cane formed on a tip-rooted cane is similar in some ways to the laterals formed further back along the parent cane. Both are partially dependent on the parent cane's reserves. Growth of the daughter cane is, however, much greater than that of a lateral in a similar position. The new plant thus appears to be a more effective "sink" than a developing lateral. The experiments showed that lateral growth on the parent cane could be affected by the presence of a daughter plant and vice versa, although the effects were small. The terminal section of the parent cane, which is able to supply most of the requirements of the daughter cane, normally bears only a

few laterals, hence competition between laterals and daughter plant may be reduced.

VEGETATIVE AND FLORAL REPRODUCTION IN WYTHAM

OCCURRENCE OF TIP-ROOTED STEMS IN WYTHAM

176. During the sampling of bramble growth in A, B and C a record was kept of any plants that had tip-rooted the previous autumn(^{P.98} Table 32).

In areas of bramble regrowth in B there were more tip-rooted stems than in the uncleared bramble, while in area D almost all canes tip-rooted.

177. TIP-ROOTING AND VIGOUR OF GROWTH A had the most vigorous bramble growth, both in terms of dry-weight per unit area and size of cane, D the least. The regrowth areas within B were less vigorous than the uncleared bramble. Thus the distribution of daughter plants fits with the work of Barnola (1971) on tip-rooting by individual canes.

178. CANOPY STRUCTURE AND TIP-ROOTING Juvenile "rooting" stems were produced by canes in A, but frequently did not reach the ground, even though some were over a metre long. The bramble in A was far denser, in terms of the interlacing of stems, than in the other areas. Thus there were far more stems tending to support a "rooting" cane, which reduced the chance of it reaching the ground before external conditions, or internal controls, brought its growth to an end.

179 In a part of area B from which the bramble was cleared away in autumn 1974, the effect of supporting structure on the number of canes tip-rooting, was examined. Six 3m X 3m areas were marked out in spring 1975 before any cane growth had begun. Three were covered by beech branches and

TABLE 32

OCCURRENCE OF TIP-ROOTED
STEMS IN WYTHAM

	Area - A	B	C	
Harvest plots	0	0.05	0.22	frequency/sq.m
Regrowth (cleared 1973)		1.33		..

TABLE 33

EFFECT OF SUPPORTING STRUCTURE
ON TIP-ROOTING

	Total stem no.s	No. rooting	% Rooting	
Controls	47	11	23	per 3x3m area
	49	9	18	
	57	11	19	..
Areas with branch covering	42	2	5	..
	48	6	13	..
	51	14	27	..

TABLE 34

VEGETATIVE & FLORAL REPRODUCTION
IN AREAS A,B,C.

	Area A	B	C	
Floral weight	24.0	2.5	0.6	g/sq.m
Frequency of tip-rooted canes	0	0.05	0.22	per sq.m

twigs (less than 2cm diameter) to form a loose network 30-40cm deep.

This was to simulate the network of stems that a first-year cane grows through in uncleared bramble. In autumn of that year the numbers of canes that had tip-rooted in the six areas were counted (^{P. 98} Table 33). In two of the covered areas tip-rooting was reduced relative to the control area.

180. ESTABLISHMENT OF DAUGHTER PLANTS IN THICKETS The interior of a bramble thicket does not appear to be less favourable for establishment of daughter plants than open areas. Daughter plants were found within a few centimetres of established rootstocks. Amor (1974 a) suggests conditions within a thicket may be more favourable for successful tip-rooting. There is a moister microclimate and the litter layer may provide a ready source of nutrients for the daughter plant. The thicket also gives protection against animals that might uproot or eat the young growth.

RELATIVE ABUNDANCE OF FLORAL AND VEGETATIVE REPRODUCTION

181. RUBUS CAESIUS RESULTS Abrahamson (1975) found that for R. caesius the relative amounts of vegetative and floral reproduction varied with the density of growth at that site. The ratio $\frac{\text{bud, flower and fruit weight}}{\text{dry weight of stem-tip layers}}$ for a plot increased with increasing density of the site. There was a strong tendency for the two forms of reproduction to be complementary with vegetative reproduction predominating at low density sites and floral reproduction in high density areas.

182. WYTHAM RESULTS The same trend was seen for areas A, B and C in Wytham (^{P. 98} Table 34) if density is interpreted as total amount of stem material present rather than just numbers of plants, per unit area. Area

D which had a lower stem density than C had a higher frequency of tip-rooting and lower floral production. Regrowth areas in B similarly showed reduced flowering and increased tip-rooting, relative to the more dense uncleared bramble.

DISCUSSION

183. **DAUGHTER PLANTS AND SEEDLINGS** The daughter plant has, in the parent cane, a much larger food base than the seedling. Amor (1974 a) found that a greater proportion of the early growth by daughter plants was as roots compared to early seedling growth. A higher proportion of daughter plants than seedlings survived their first year of growth. Because of its higher reserves a daughter plant is more likely to be able to establish under unfavourable or competitive conditions, such as in grassland.

184. **THICKET FORMATION** Spread by tip-rooting of canes can lead to rapid development of a dense thicket from a few original rootstocks. This was described for R. procerus by Amor (1974 a). He found that outward spread of a thicket at one site was 3.3m a year.

185. During initial invasion of a site, the bramble density is low and vegetative reproduction advantageous because of the speed with which a thicket can be formed. Once a thicket is formed, vegetative reproduction is less of an advantage as intra-specific competition is high. Greater floral reproduction relative to vegetative spread, characteristic of high density sites, increases the chances of colonisation of a new site.

186. **REPRODUCTION ON MARGINAL SITES** On sites such as D which are marginal for bramble growth, unfavourable conditions keep stem density low. Individual plants grow less and death of rootstock is more likely. Vegetative reproduction is more effective at maintaining the numbers of

plants because the greater food base of the daughter plant increases its chances of survival relative to those of a seedling.

187. REGULATION OF REPRODUCTION The complementary nature of the two forms of reproduction in different areas of Wytham suggests that both may be controlled by the same factor. This might be external such as the level of light increasing flowering, but decreasing root boss formation. Internal controls are also involved.

188. Strongly growing canes are less likely to form juvenile "rooting" stems than weak canes. In addition vigorous canes tend to form dense thickets. These often make the canes more upright reducing their tendency to tip-root, and also reduce the chances of any rooting stem that is formed reaching the ground.

189. On the other hand vigorous canes produce long laterals, which are more likely to flower and fruit than laterals borne on weak canes. There appears to be some competition between growth of a daughter plant and that of laterals. Any reduction in tip-rooting may thus increase the reserves available for lateral growth and flowering.

190. TIP-ROOTING AND "WEEDINESS" Cane tip-rooting is one of the characteristics that makes Rubus fruticosus a weed. Amor (1973) showed that the tendency with which different bramble species formed tip-rooting stems was a major factor in distinguishing those species that were classed as weeds in Australia from those that were not. Some of the results obtained in Wytham on occurrence of tip-rooting and daughter-plant development may help in tackling the bramble weed problem.

NON-DESTRUCTIVE SAMPLING

191. INTRODUCTION The destructive sampling of bramble in areas A, B and C during 1974 provided an opportunity for comparing the effectiveness of different non-destructive methods of measuring bramble. Such measurements can be made repeatedly at the same point without altering the growth there. Destructive sampling alters subsequent growth; regrowth is less vigorous and the surrounding bramble canopy is disturbed.

MEASUREMENTS OF INDIVIDUAL STEMS

192. STEM LENGTH Stem lengths provide a measure of their growth. Measurements made on individual canes and laterals were converted to an area basis by using the mean density of canes per unit area. The contribution of the standing dead to total stem length was calculated using rates of turnover for this component derived earlier, page 48 .

P.103

Table 35 shows estimates of total stem length per unit area, derived in this way, together with actual stem lengths per plot at Harvest 6.

193. LEAF COVER Leaf cover was found to be similar in A and B. Table 36 shows that differences in the numbers of stems per unit area were offset by the differences in individual stem length, and hence numbers of leaves per stem. Final leaf numbers per plot were thus similar. Leaflet diameters were the same and as this was closely correlated with leaflet area (Figure 30)^{P.104} leaf area per plot was thus similar for the two sites, A and B.

194. WEIGHT-ON-LENGTH REGRESSIONS Regressions of dry weight on

TABLE 35

ESTIMATED AND MEASURED
STEM LENGTH/SQ.M

Table 35

Area	A	B	C	
Measured (Harvest 6)	49.8±5.7	36.1±2.6	21.9±3.7	metres
Estimated	56.4	35.5	18.0	"

TABLE 36

LEAF NUMBERS PER METRE-SQUARE

Table 36

<u>Canes.</u>			
Area	No of 1st yr.s per metre-square	Leaf nos/cane	Leaves/sq.m
A	3.1	23.2	71.9
B	5.1	14.7	74.8

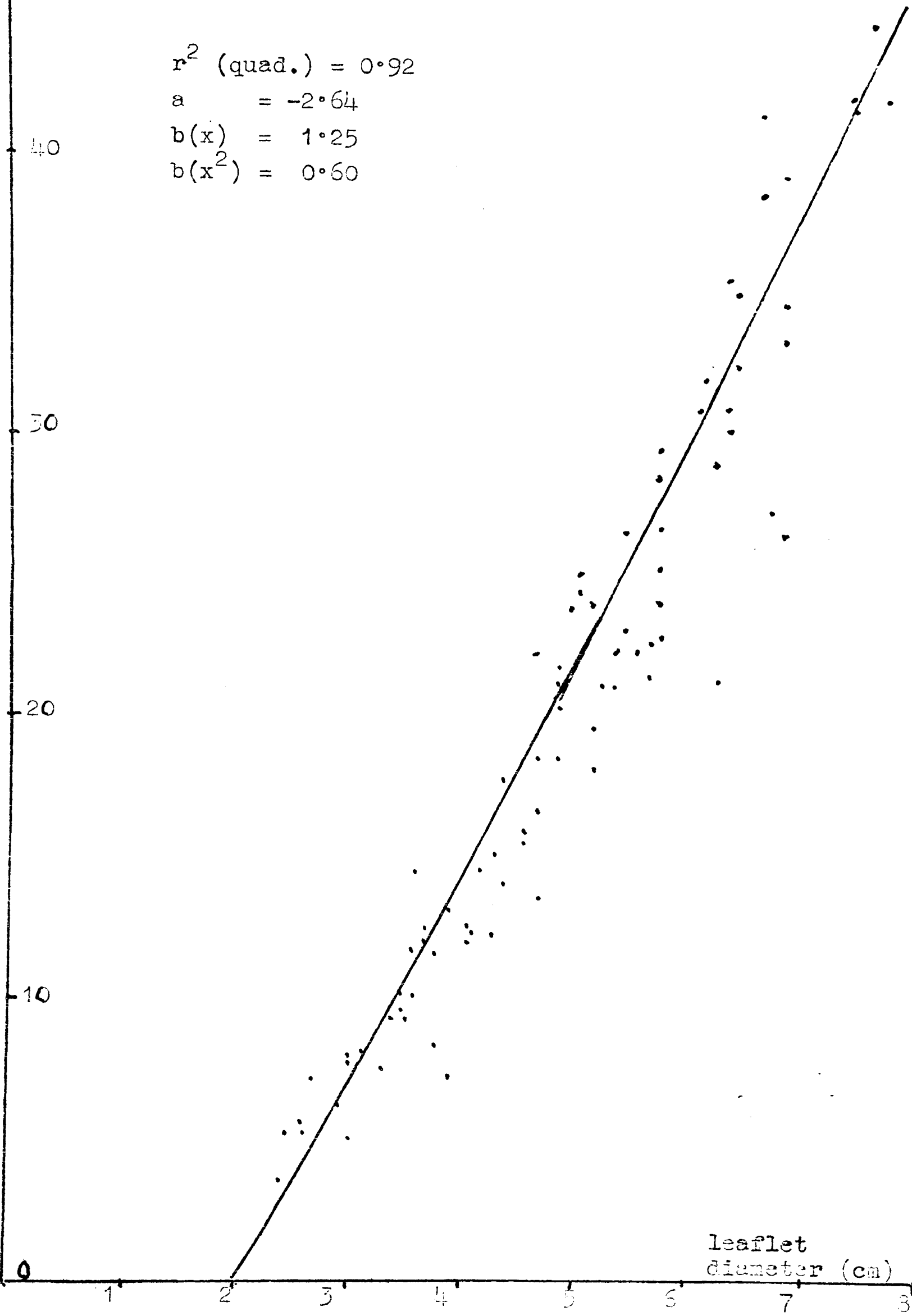
<u>Laterals</u>			
	No of laterals per metre-square	Leaf nos/lateral	Leaves/sq.m
A	53.0	7.9	418.7
B	52.5	6.5	330.9

Mean leaflet diameters A 57.5 ±2.2 mm
B 57.5 ±1.4 mm

REGRESSION OF LEAFLET AREA ON
DIAMETER

leaflet
area

r^2 (quad.) = 0.92
a = -2.64
b(x) = 1.25
b(x²) = 0.60



stem dimensions have been widely used in forestry for estimating tree biomass. Bunce (1968) derived similar equations for undergrowth species including bramble and bracken. From equations of this sort the dry weight of bramble in a plot could be calculated if the dimensions of stems in that plot were measured. The denseness and size of some of the bramble stands in Wytham would have made such measurements very difficult without considerable disturbance of the stand.

AREA MEASUREMENTS - INTRODUCTION

915. Measurements made on an area basis are an integration of the growth of the various stems in the plot. There is no direct measure of the relative contributions of lateral and cane growth to the overall changes observed. Growth within the plot may be influenced by conditions acting on sections of cane outside the plot. Plot measurements have the advantage that precisely the same point is recorded each time. The same paths can be used to reach the plot thus keeping disturbance to a minimum.

196. To test and calibrate the methods used, all the harvest plots in A, B and C were "recorded" immediately before they were cut. Five permanent plots, each a metre-square, were also set out in each of the three areas. These were recorded during 1974 for comparison with the harvest plots and during 1975 to look for year-to-year variation.

197. The methods used were point quadrats, for determining the quantity and distribution of leaves, and Intersection Values. These latter were used to estimate the length of stem in a plot and also the total dry-weight of bramble present.

POINT QUADRATS

INTRODUCTION

198. Point quadrats give an estimate of the leaf area present in a plot. The nature of the estimate, relative to total leaf area, depends on the size and angle of the pins and on the angle of the leaves themselves.

199. **SIZE OF PIN** Thick pins tend to lead to over estimation of the leaf area. The degree of error involved depends on the dimensions of the leaves. (Warren-Wilson 1963). 1.5mm pins were used in this study and only tip-contacts recorded. For mature leaflets of dimensions, 50 X 55mm, the theoretical error was about 6%.

$$\text{Error} = \frac{d \times (1+b)}{lb}$$

d = pin diameter
l = leaf length
b = leaf breadth

The error was greater for smaller leaflets, but still small compared to other sources.

200. The narrower the pin the greater the lashing movement of the tip as it gets further from the bottom of the frame. In Wytham the bulk of the bramble canopy at any one point was within 30cm of the frame, although overall canopy depth was often greater. Sideways movement of the tip was thus not very great.

201. **ANGLE OF PINS** Warren-Wilson (1960) showed that, where leaf angles varied, the most consistent estimates of leaf area from point quadrats were obtained using pins inclined at 32.5° to the vertical. Vertical pins were, however, much easier to use, particularly in the

taller bramble stands in Wytham. The number of hits recorded was thus a measure of the effective horizontal area of leaf in that plot.

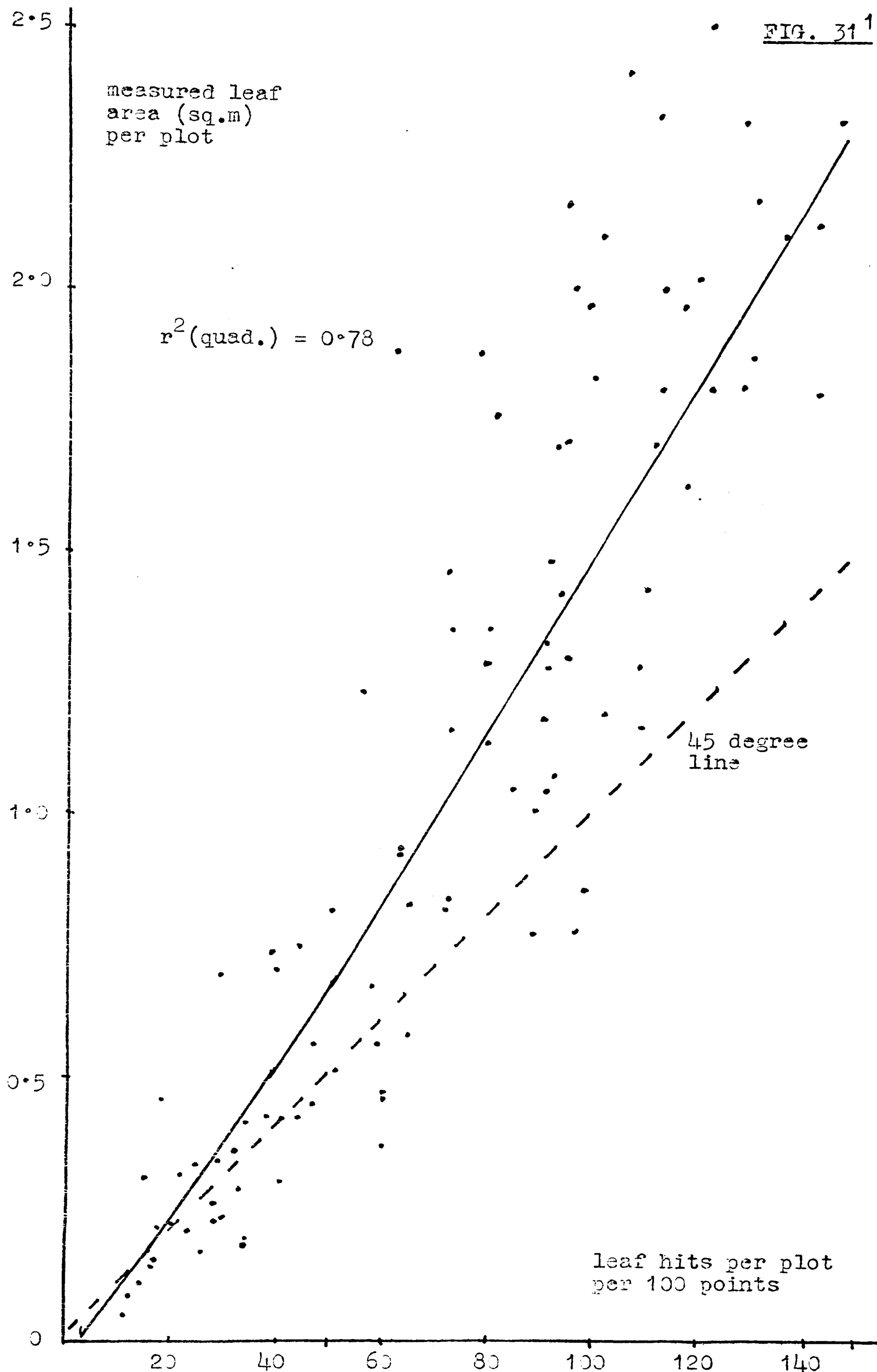
THE RECORDING PROCESS

202. **DISTRIBUTION OF POINTS** The frame used was 50cm long with 10 holes at 5cm intervals. It was fixed in the ground by a central spike. The spike was placed at random in a plot by using a system of approximate coordinates and random numbers. The frame was then orientated at random in any one of six directions, corresponding to 1-6 on a clock face.

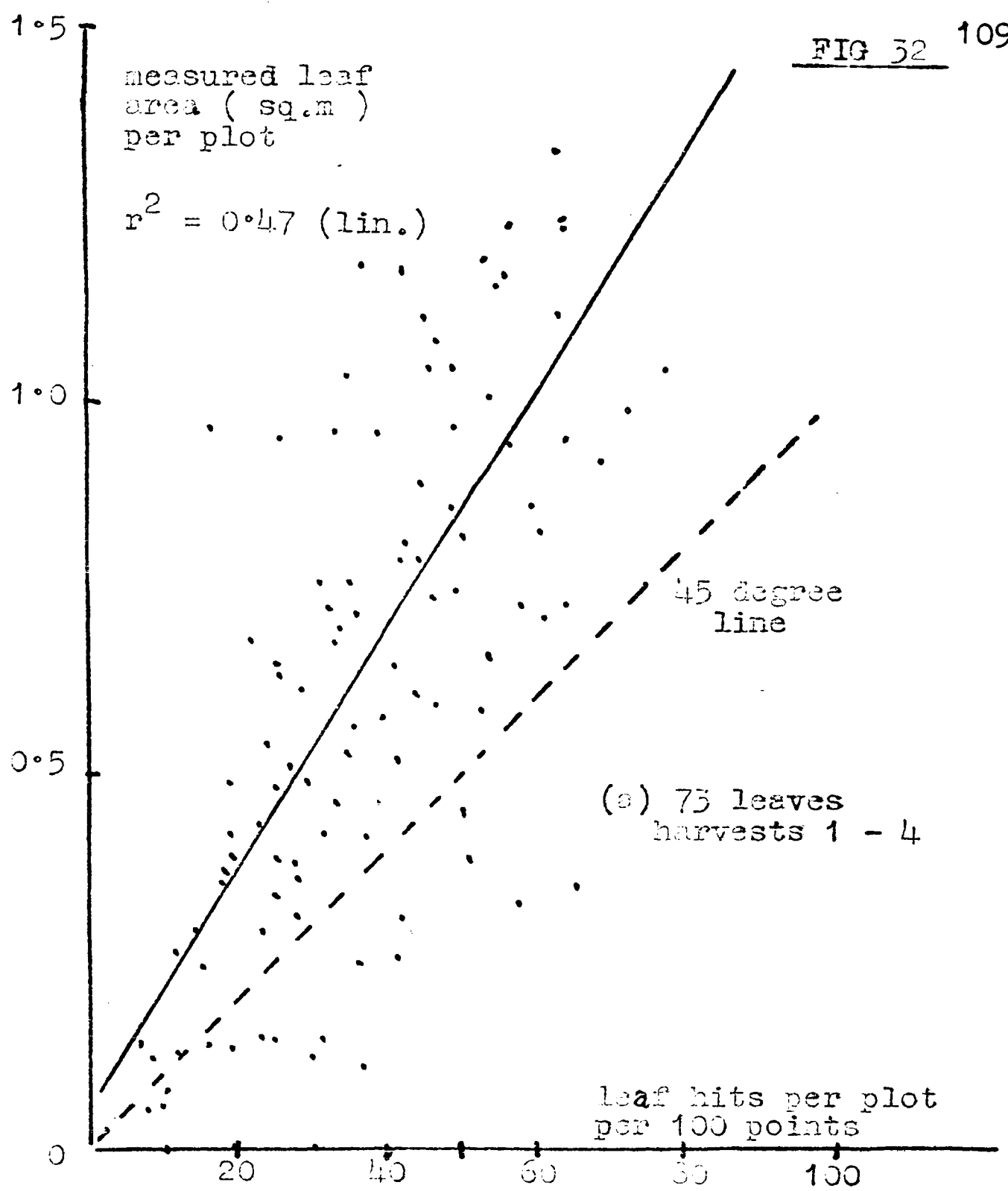
203. All ten points per frame were used so that the plot was sampled by a series of random lines of points. From ten to twenty positions of the frame were needed per plot, depending on how many of the points fell outside the plot, to give a total of 100 points/sq.m. This number was chosen by observing the trend in mean hits per ten points for successive additions of ten points. (Grieg-Smith 1964). Use of only one point per frame rather than all ten was shown to require fewer total points to obtain the same precision of result (Winkworth 1955). Because of the greater number of times the frame has to be moved, this would have required a longer time per plot in Wytham.

204. **HITS RECORDED** All contacts, not just the first per point, were recorded. Initially both leaf and stem hits were noted, but later stem hits were abandoned. Leaves of the current-year's growth were distinguished from those of the previous year. No attempt, however, was made to separate cane leaves from lateral leaves.

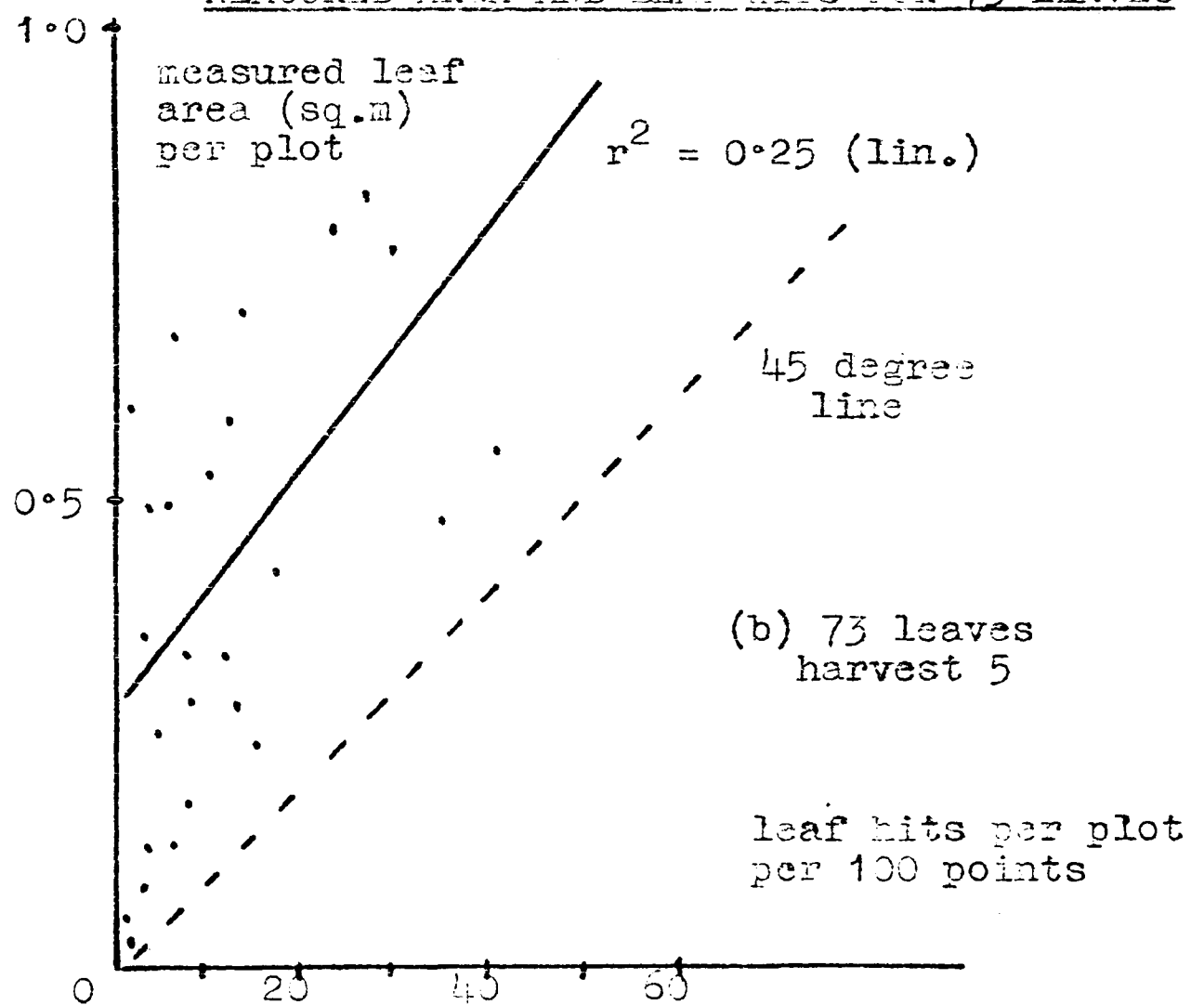
205. **HEIGHT OF HITS** The height of each hit was recorded and used to prepare canopy profiles. A second pin, graduated in centimetres,



REGRESSION OF MEASURED AREA ON HITS FOR 74 LEAVES
(harvests 5 - 8)



MEASURED AREA AND LEAF HITS FOR 73 LEAVES



was lowered alongside the original pin. The height of leaves relative to each other was more important than their absolute distance from the ground directly beneath them. Measurements were made therefore of the distance of the leaf from the frame, and mean height of the frame above the ground used to convert these distances to heights. Some error was introduced when the frame was not horizontal. This was smaller than the discrepancy arising from direct measurement of the height of each leaf, because of the differences in ground level that occurred within a plot, even where there was no slope from one side to the other.

206. LEAF ANGLES The relation between effective horizontal area as measured by leaf hits and total leaf area depends on leaf angle. There was, however, no simple relation between them for bramble because leaflets frequently sloped in two directions at once and the angle of slope varied along the leaflet. An attempt was made to gain some estimate of leaf angles by using a protractor and plumb line although this was imprecise.

LEAF HITS/SQ.M. FOR THE HARVEST PLOTS

207. LEAF HITS AND MEASURED LEAF AREA For harvests 1-8, leaf hits were compared with measured leaf-area, page 21 . Regressions of leaf area on hit number are shown in Figures 31, 32. Except for the early growth of 74 leaves there was a tendency for leaf-hits to under-estimate the actual total leaf area. The under-estimation increased and correlation decreased for the 73 leaves which had survived over winter.

208. CAUSES OF UNDERESTIMATION OF LEAF AREA Errors resulting from the finite size of the pin or "lashing" movements of the pin tip tend to increase the number of leaf hits relative to the total area. Some hits were missed where the number of leaves made it difficult to follow the

FIG 33

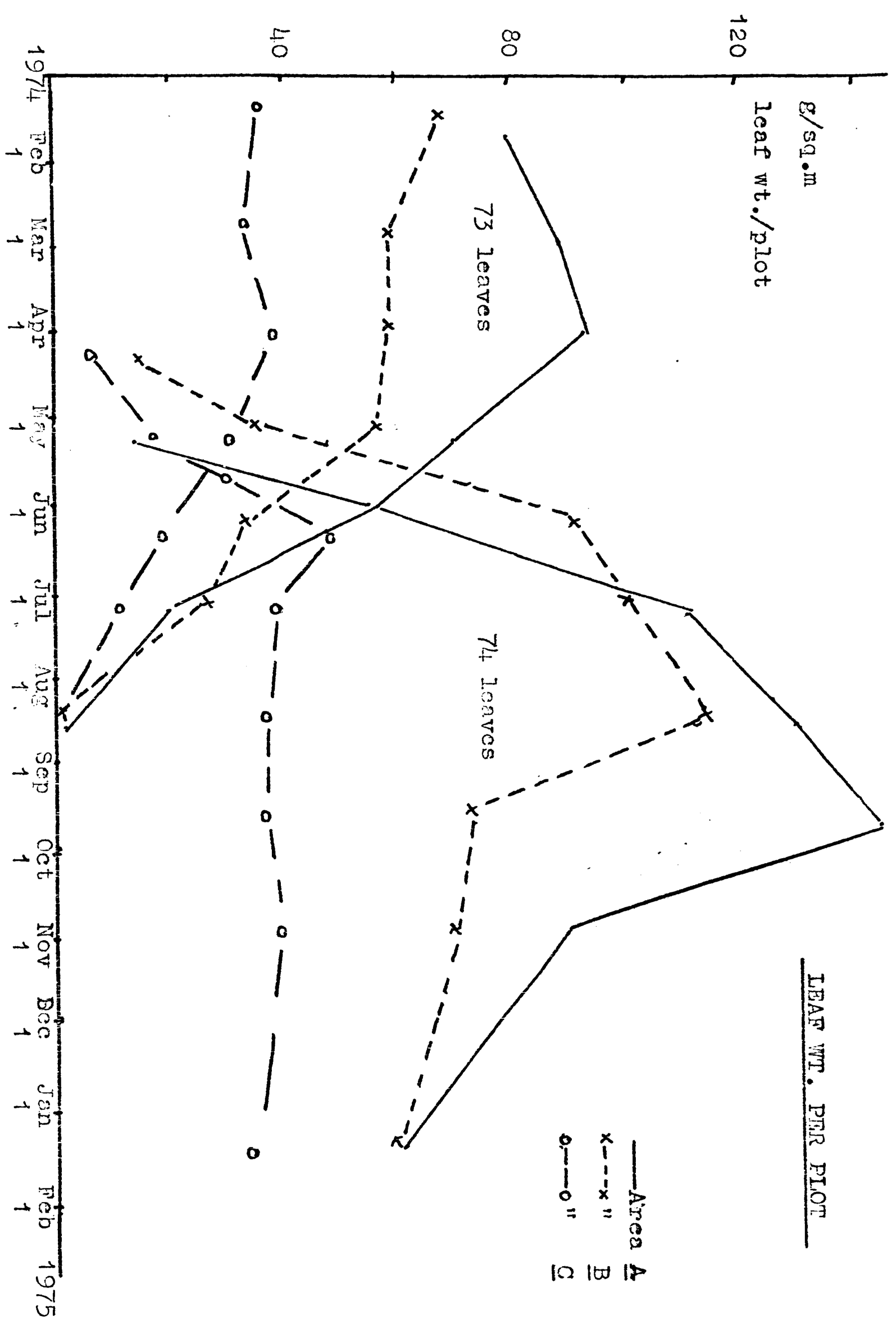


FIG 34

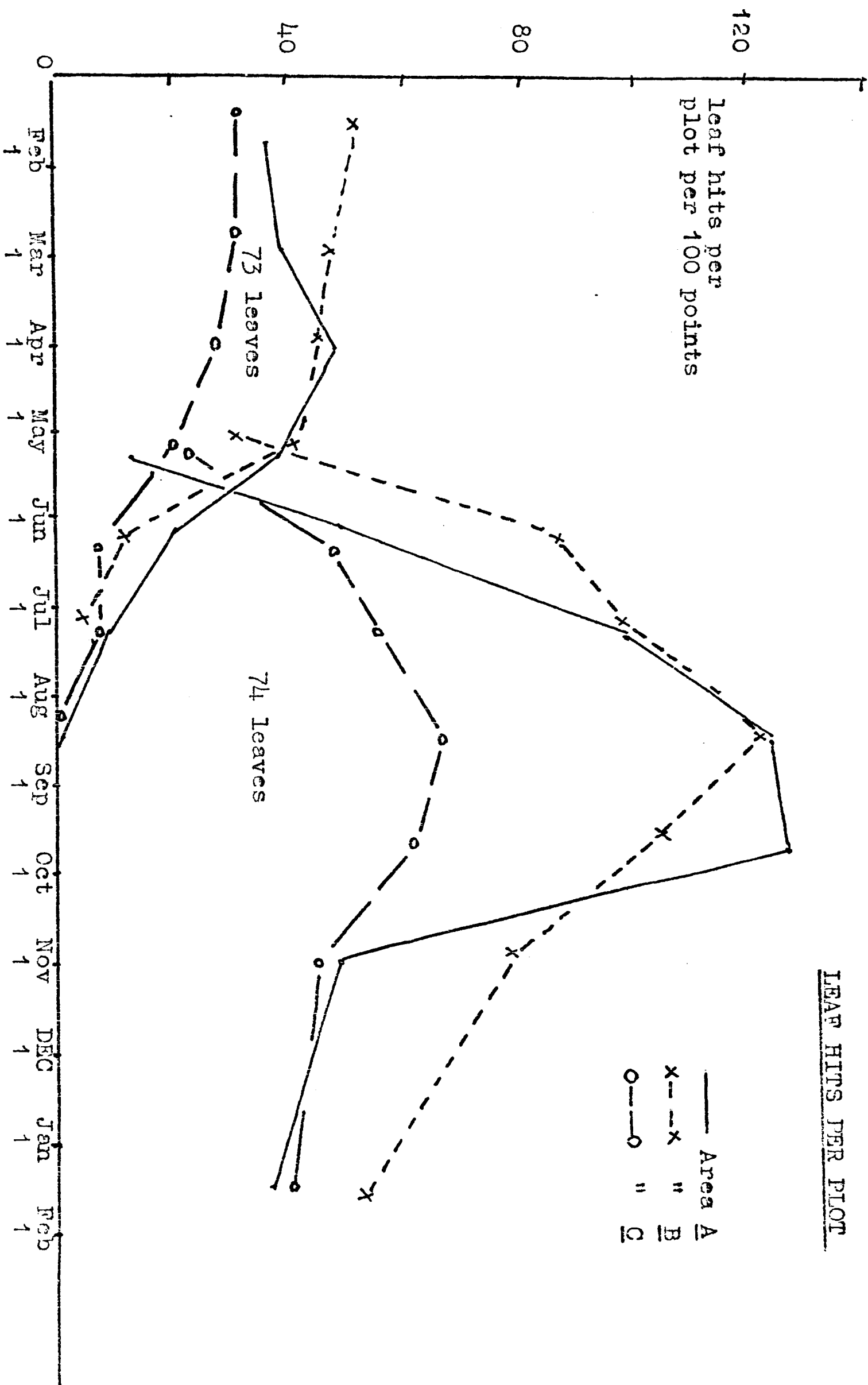
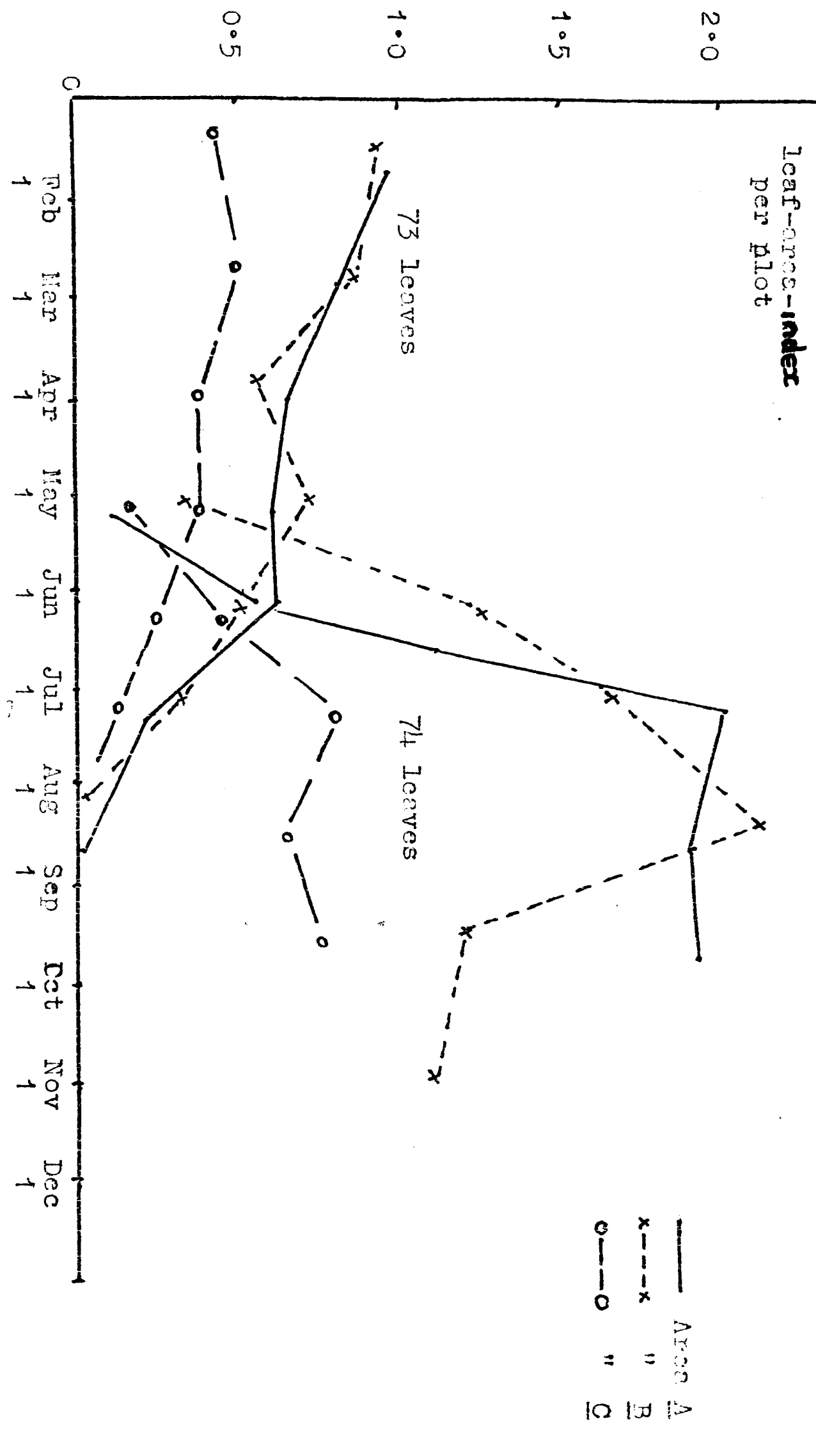


FIG 35



pin-tip down through the canopy. This may be a major factor in the poor correlation for 73 leaves at H5. The new (74) leaf canopy was well developed by this time above the older, 73 leaves. Leaf angle also contributed to the under estimation of leaf area by leaf hits and to the difference between 74 and 73 leaves.

$$74 \text{ leaves} = 16^{\circ} \quad 73 \text{ leaves} = 38^{\circ} \text{ to the horizontal}$$

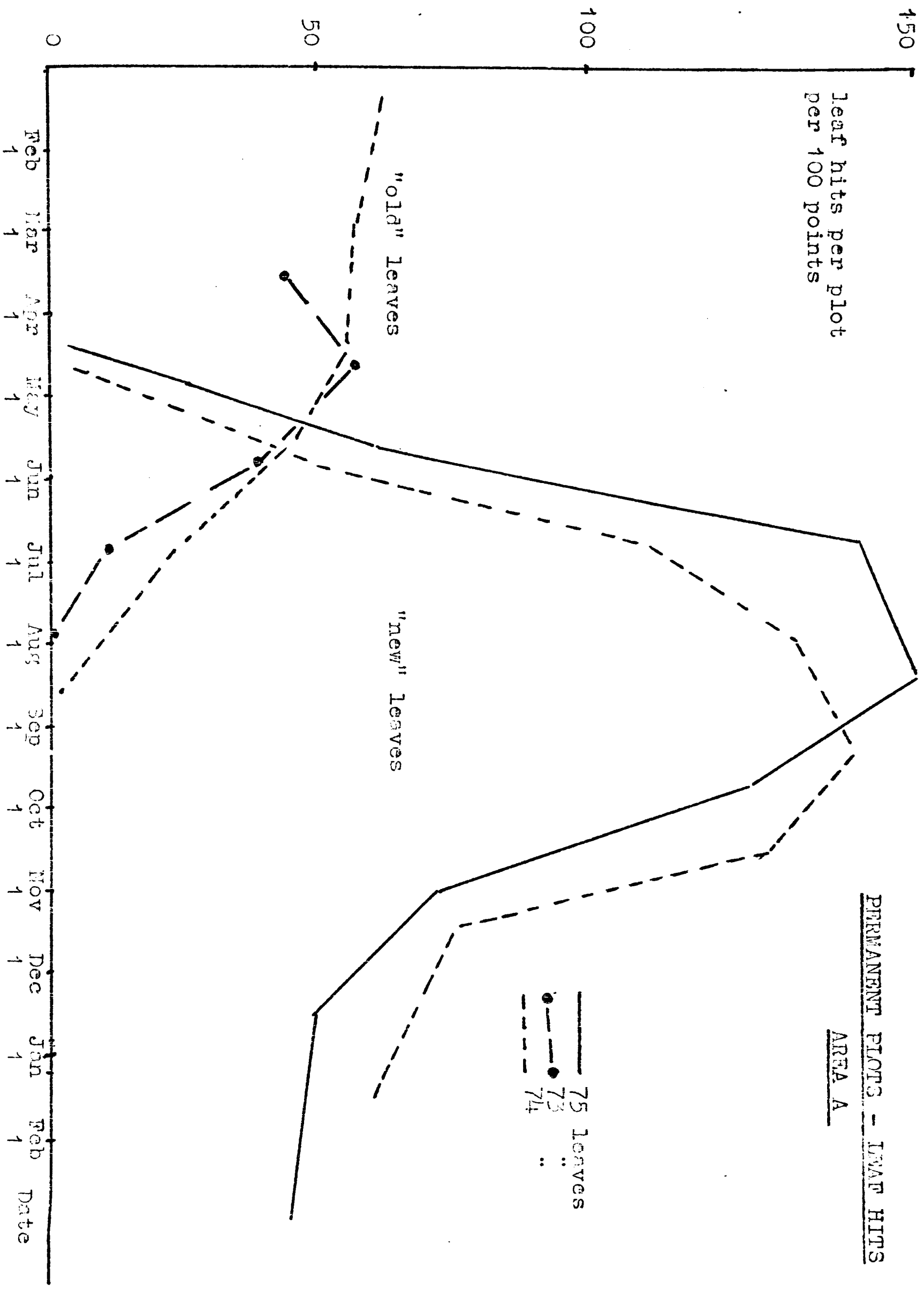
The greater leaf angle of the 73 leaves, as a result of exposure to winter conditions, increased the difference between leaf hits and leaf area and decreased the correlation between them.

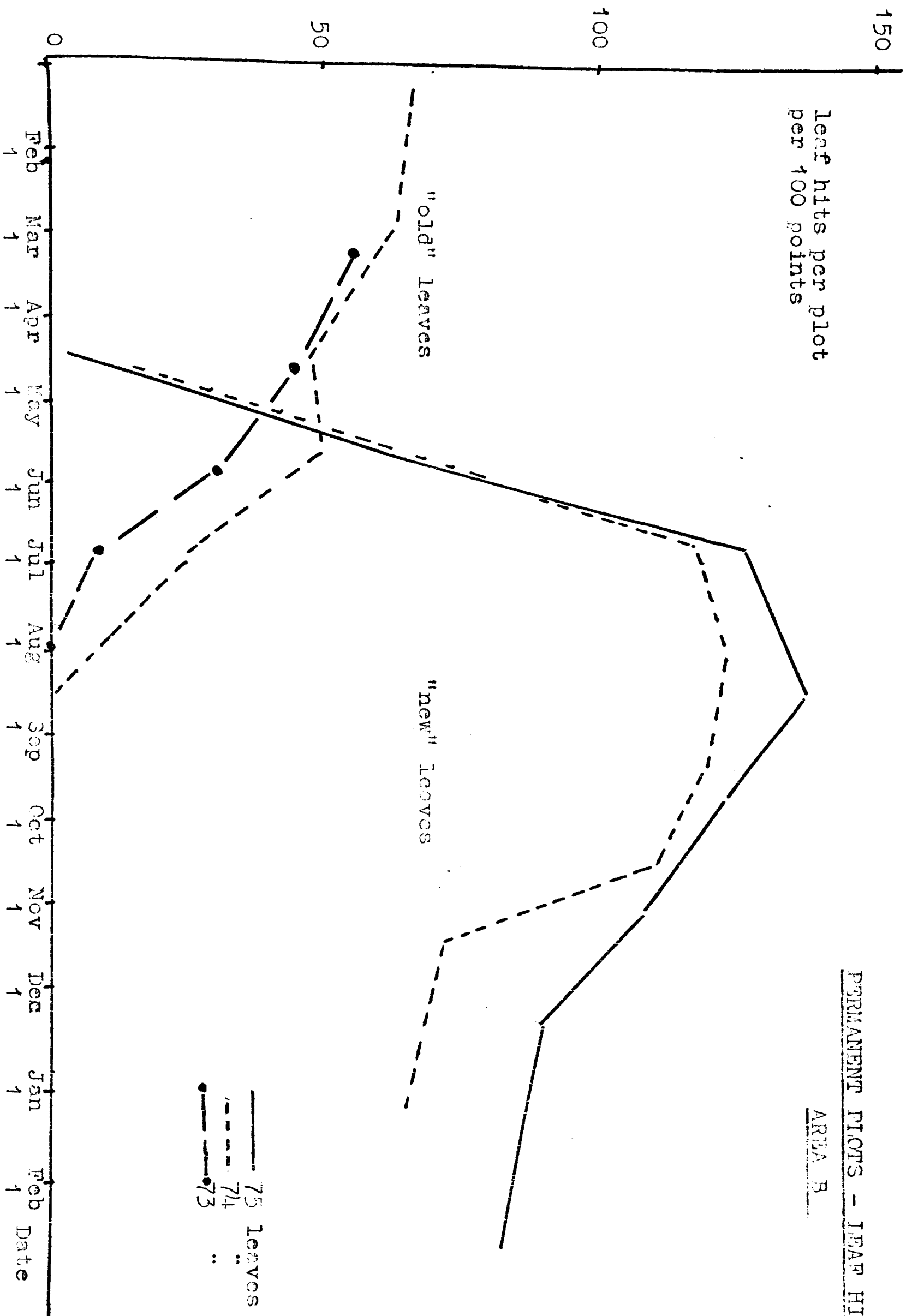
209. Leaf hit curves for the three areas were similar in shape to those for leaf weight and leaf area for the three areas. Thus leaf hits did provide a measure of the change in leaf amounts over the season.
 (P. 111, 112, 113
 Figures 33, 34 and 35).

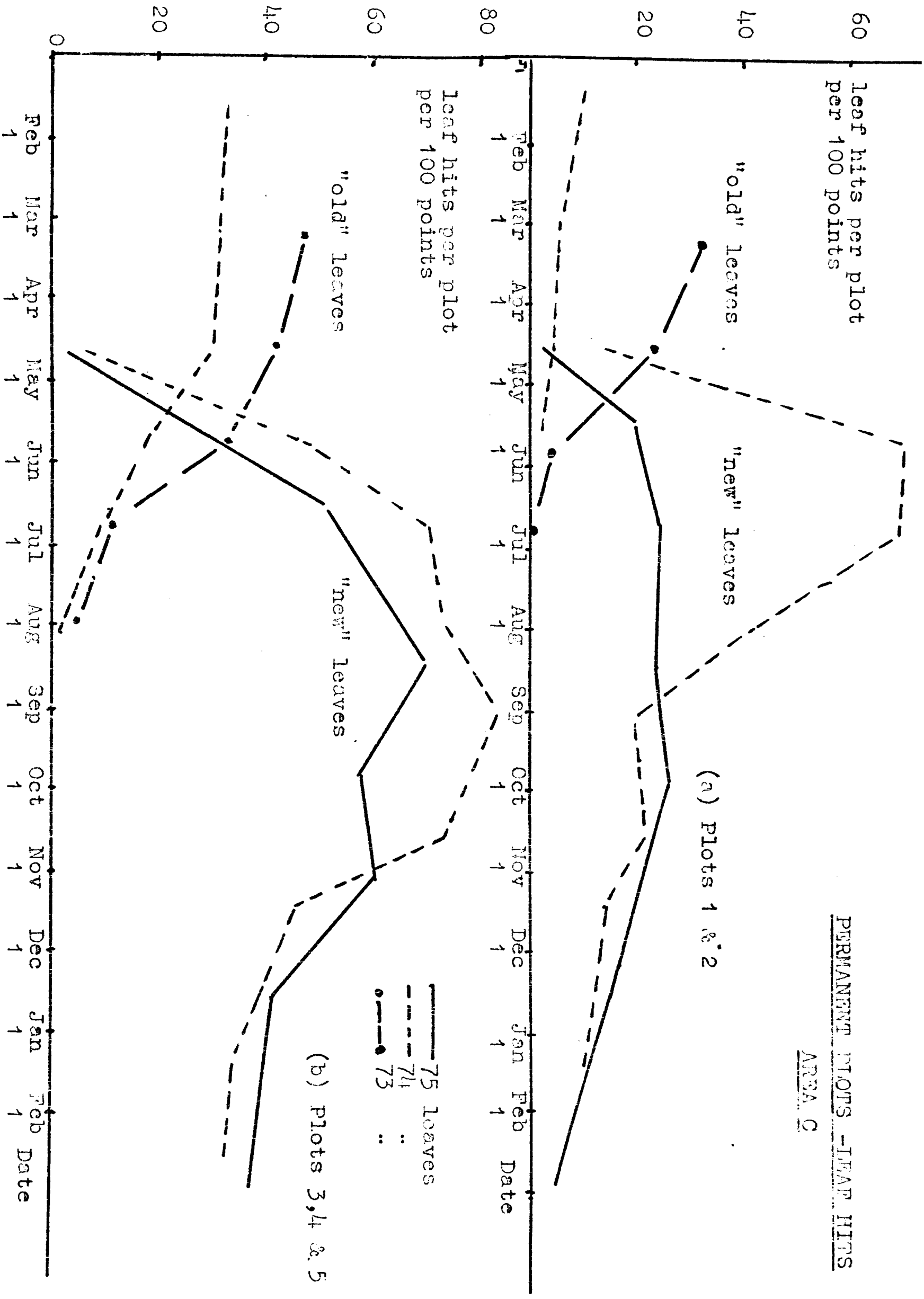
LEAF HITS IN PERMANENT PLOTS

210. AREAS A AND B There was little difference between leaf hit curves for 1974 and 1975 in these two areas (P. 115 P. 116 Figures 36 and 37). There was greater leaf survival over winter in 1975-76 in B, than was found in either of the two previous years, but there was no apparent reason for this. Leaf cover was higher than in the harvest plots, a reflection of the subjective siting of the permanent plots.

211. AREA C The curves for leaf hits in C differed in size and shape in the two years. The results for the five plots were examined individually and two patterns emerged (P. 117 Figure 38). Plots 3, 4 and 5 showed little difference between the years and were similar to the harvest







plots. In plots 1 and 2, however, a large number of leaves died off suddenly at the end of June. Some of the stems died also. The effect was very localised and appeared to be permanent as growth in 1975 was correspondingly reduced. The cause of this change is unknown.

CANOPY PROFILES

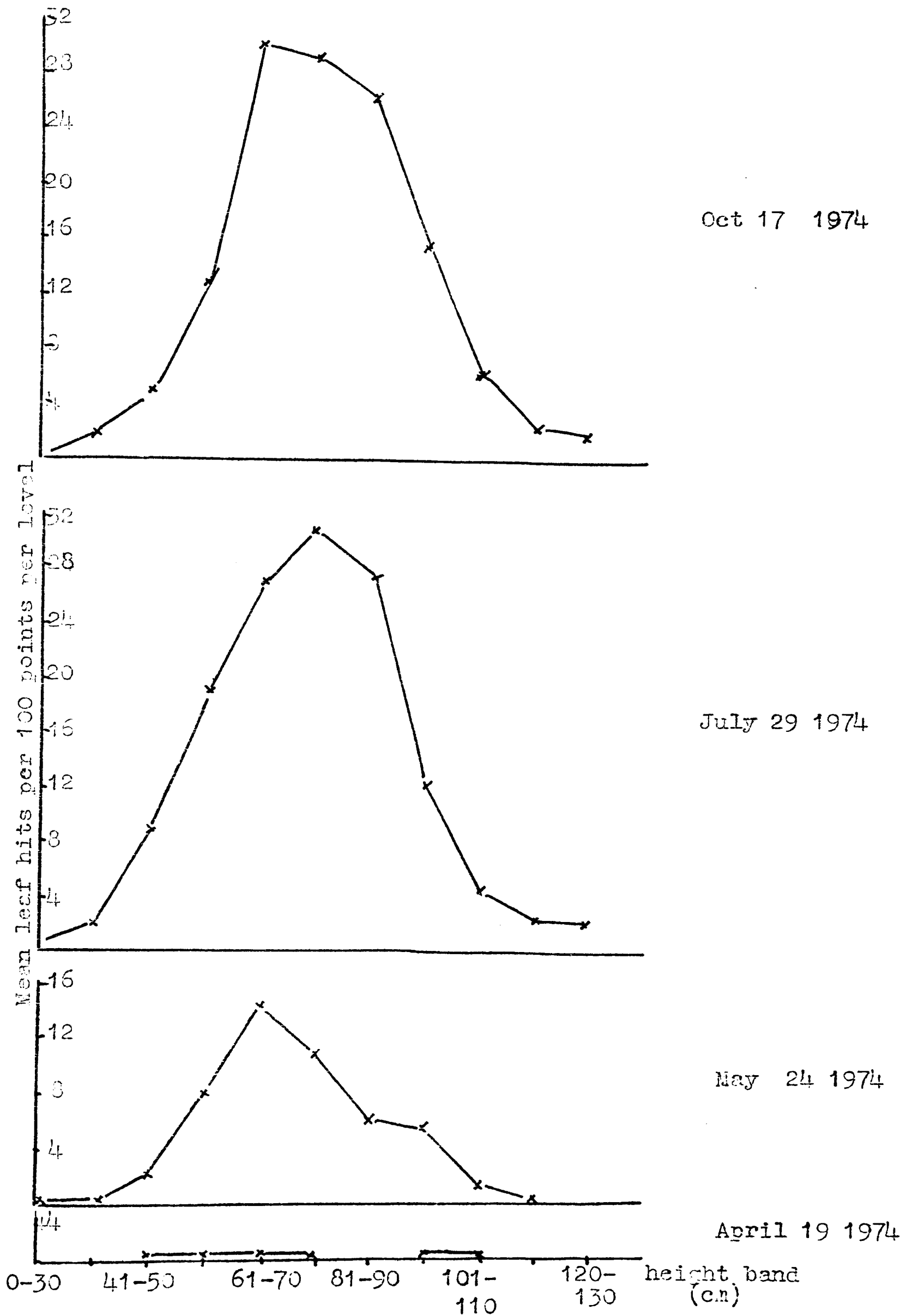
212. The heights of the leaf hits were combined in 10cm bands to produce canopy profiles. The distribution of 74 leaves is shown in ^{P. 119-122} Figure 39, from their formation in Spring 1974, to final die-back in summer 1975. The profiles are based on all five permanent plots in A and B. In C plots 1 and 2 were excluded because of the unusual leaf die-back in summer 1974.

213. **PROFILE SHAPE** Leaf hits in A and B showed a normal distribution of leaf hits with respect to height for much of the year. Partly this was a consequence of combining results from several plots. If loss of lower leaves through self-shading had occurred early in the season, a more skewed distribution would result. Ford and Newbould (1971) found a similar profile shape for a sweet chestnut canopy, although its dimensions were very different (^{P. 123} Figure 40). The profiles for area C were less regular in shape. There was a significant number of leaves in the 0-10 band for much of the year, so that the "normal" curve was truncated.

214. **A AND B SIMILARITY** The bramble canopy in A was slightly deeper than that in B and based 30cm higher. Otherwise the two profiles were very similar in shape. Differences between A and B occurred in spring 1974, when growth in A started later than in B, and in spring 1975. This difference may have been a sampling error caused by the difficulty of recording the old (74) leaves beneath the new canopy of 75 leaves.

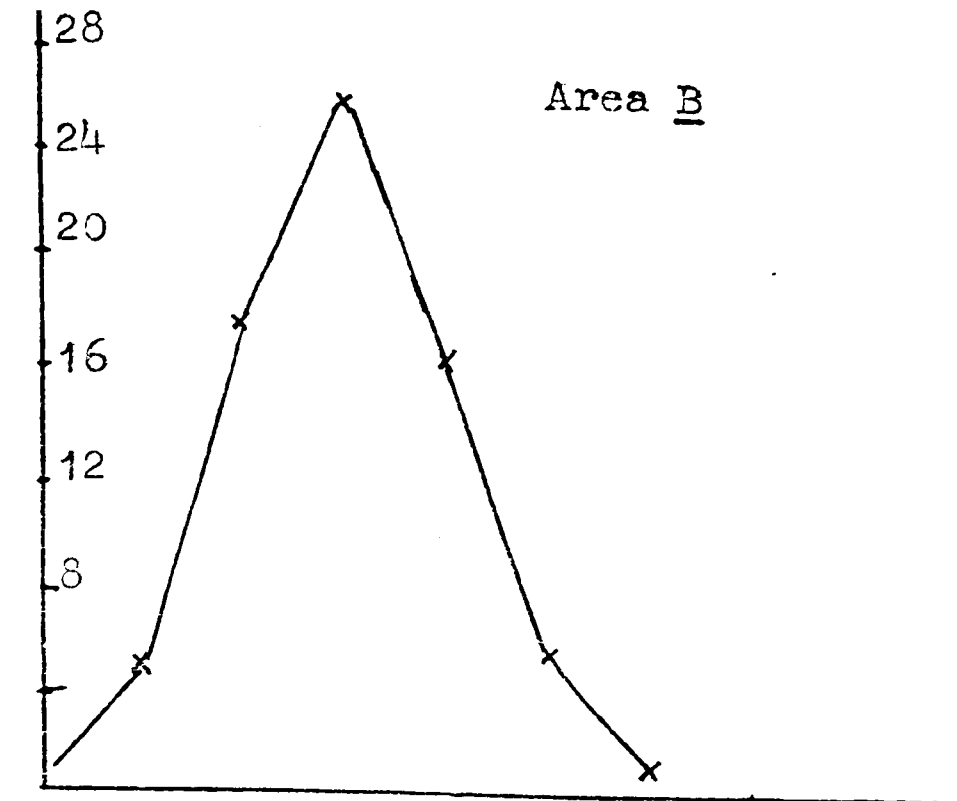
CHANGES IN THE DISTRIBUTION OF 74 LEAVES 1974-5

Area A - Based on all 5 permanent plots

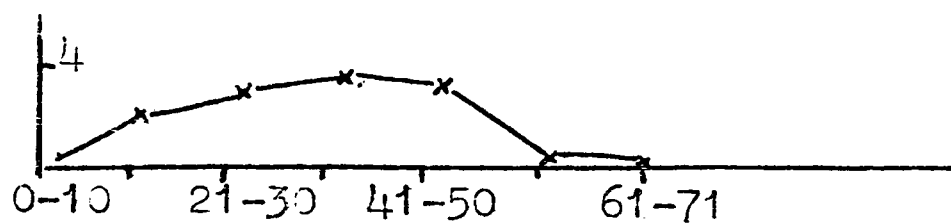


Area B

May 24 1974

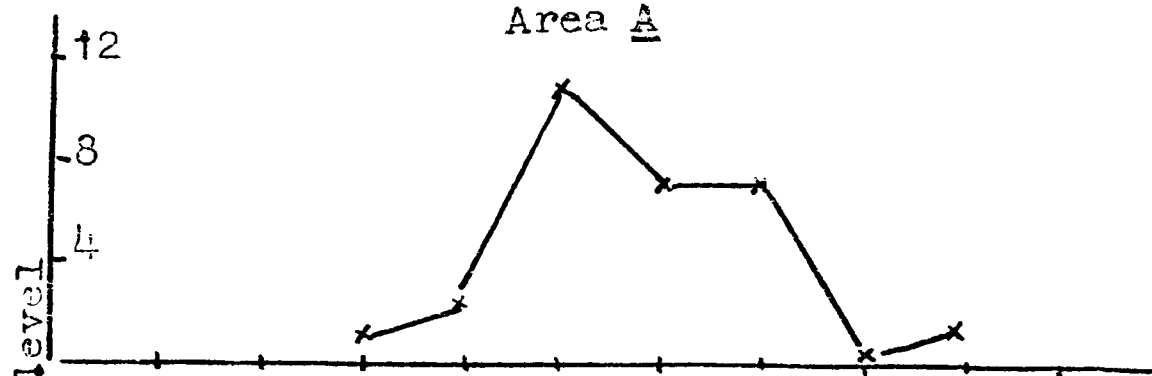


April 19 1974



Area A

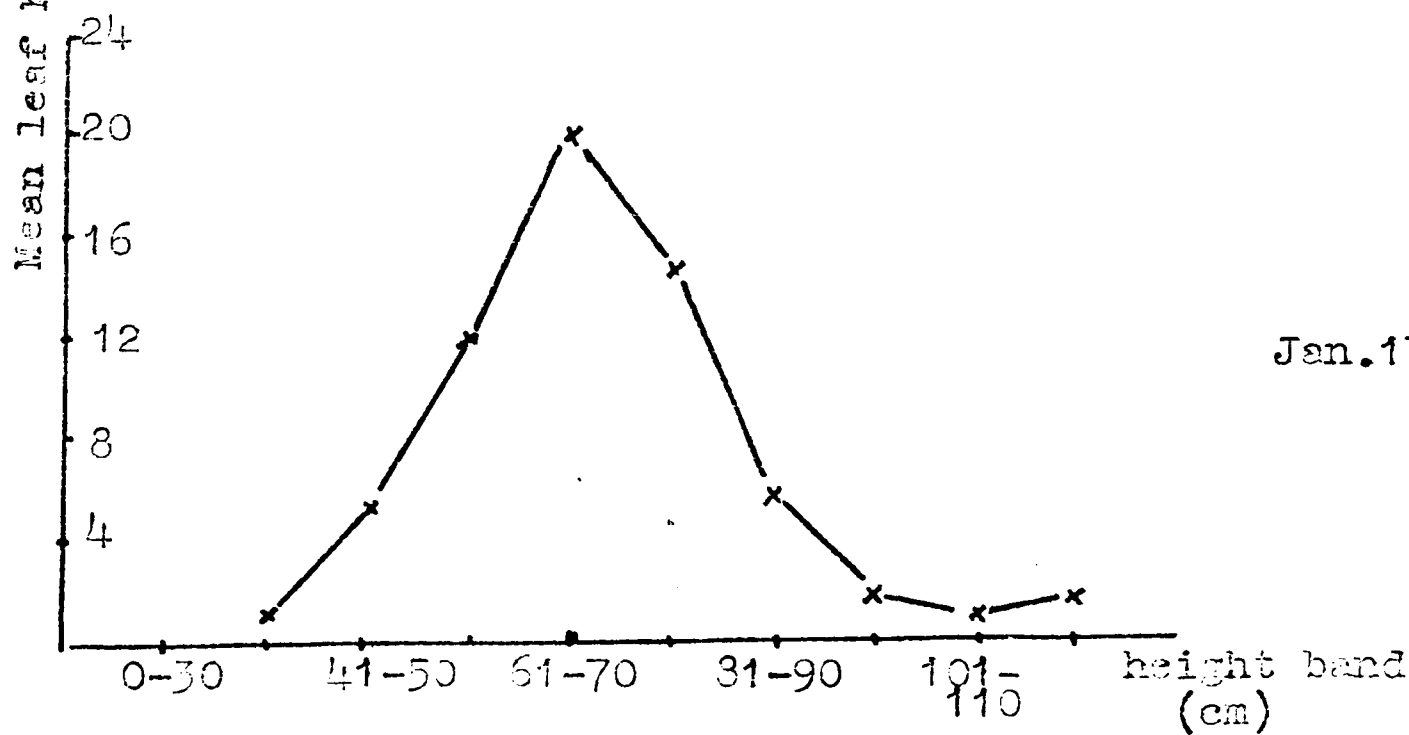
June 25 1975



April 15 1975

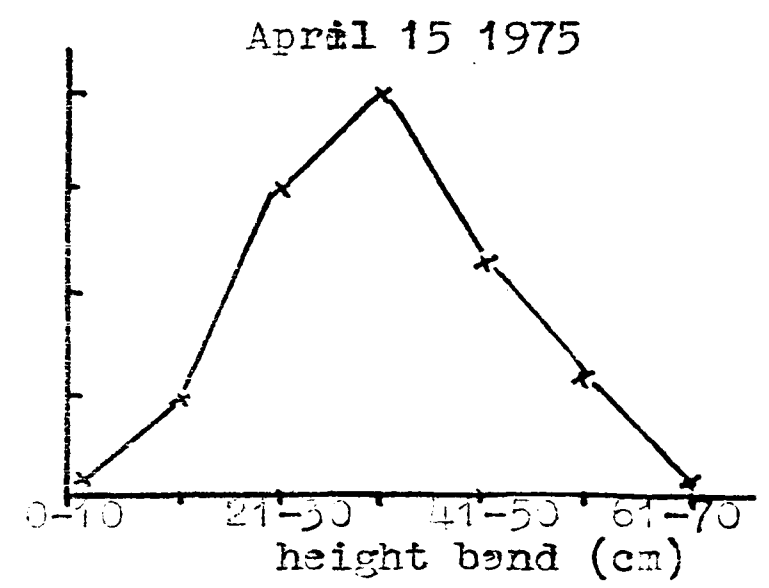
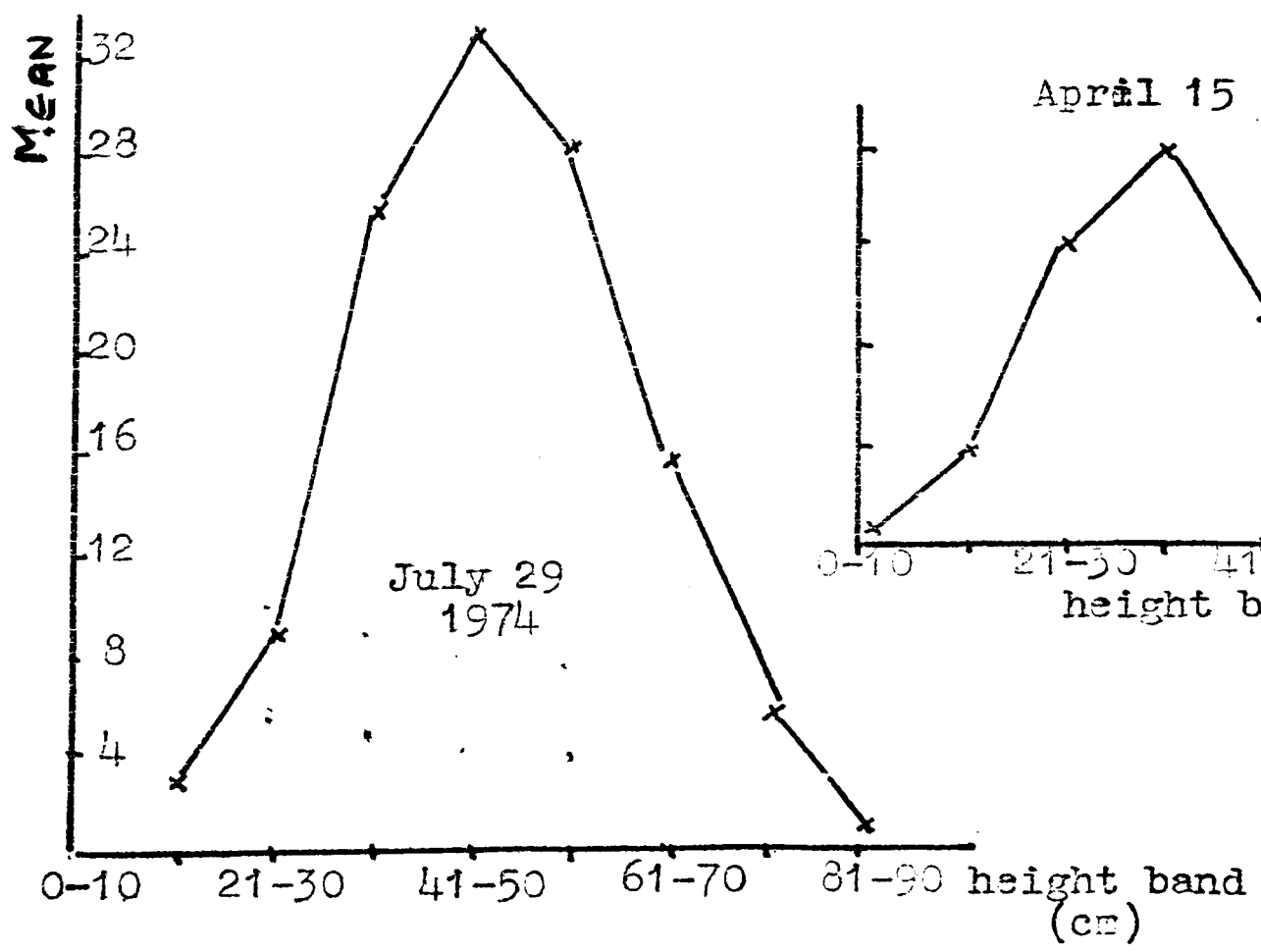
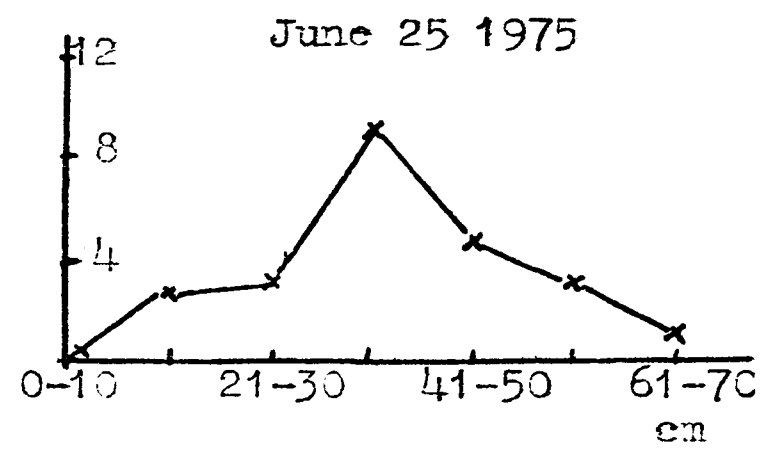
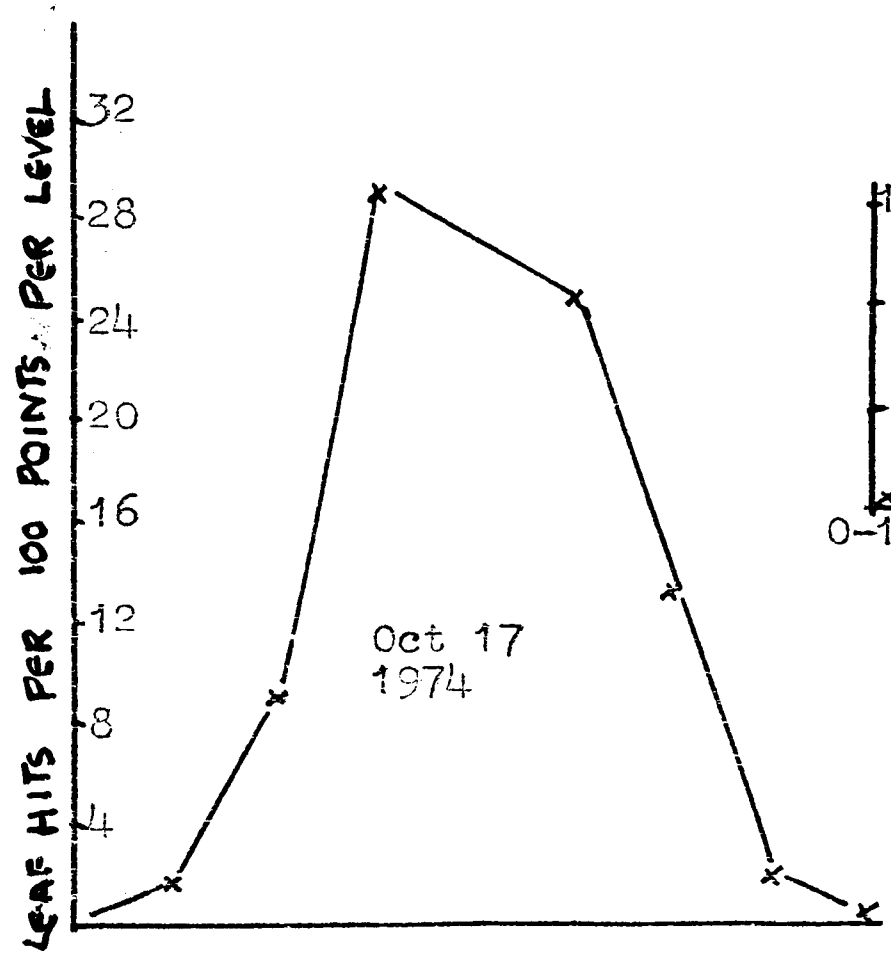
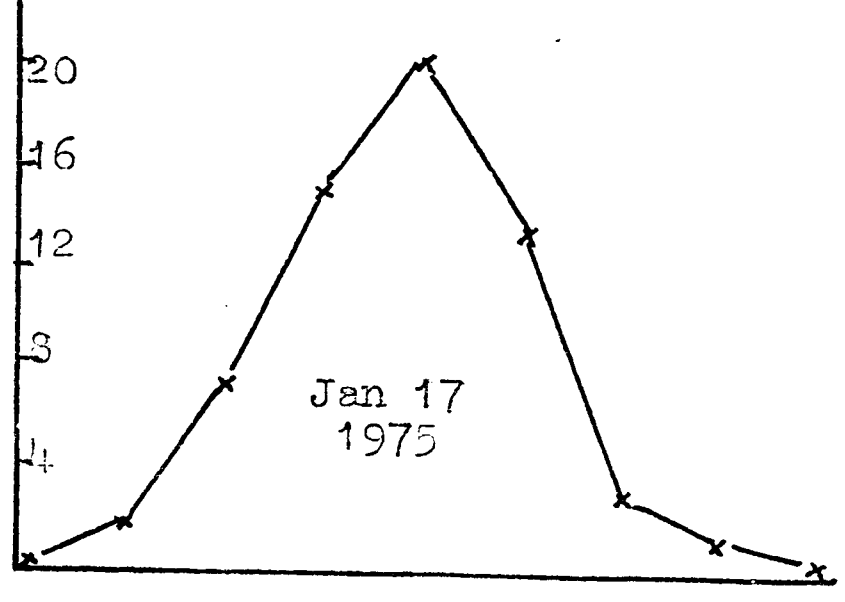


Jan. 17 1975



CHANGES IN THE DISTRIBUTION OF 74 LEAVES 1974-75

Area B - Based on all 5 permanent plots



CHANGES IN THE DISTRIBUTION OF 74 LEAVES 1974-5

Area C - Based on permanent plots 3,4,5.

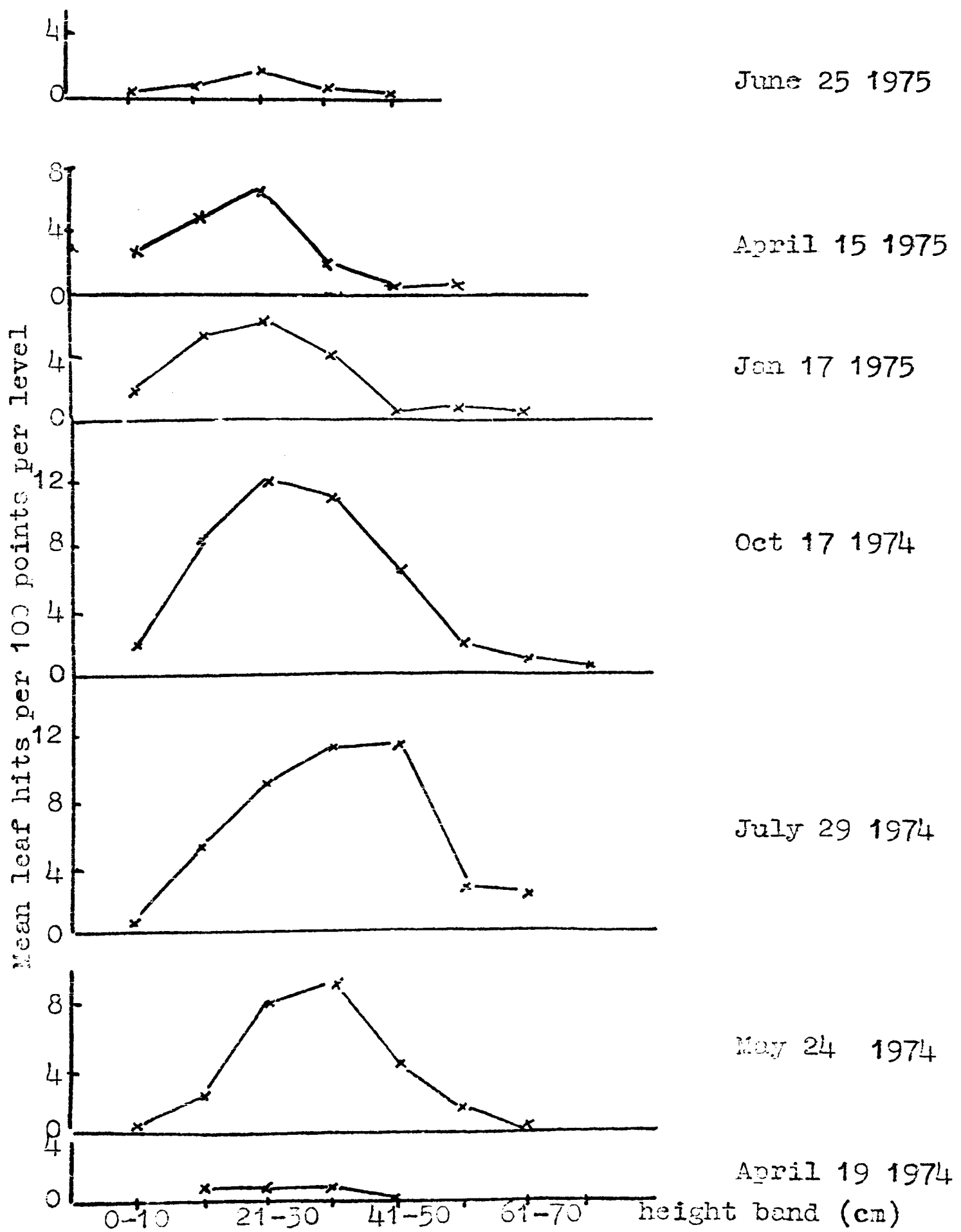
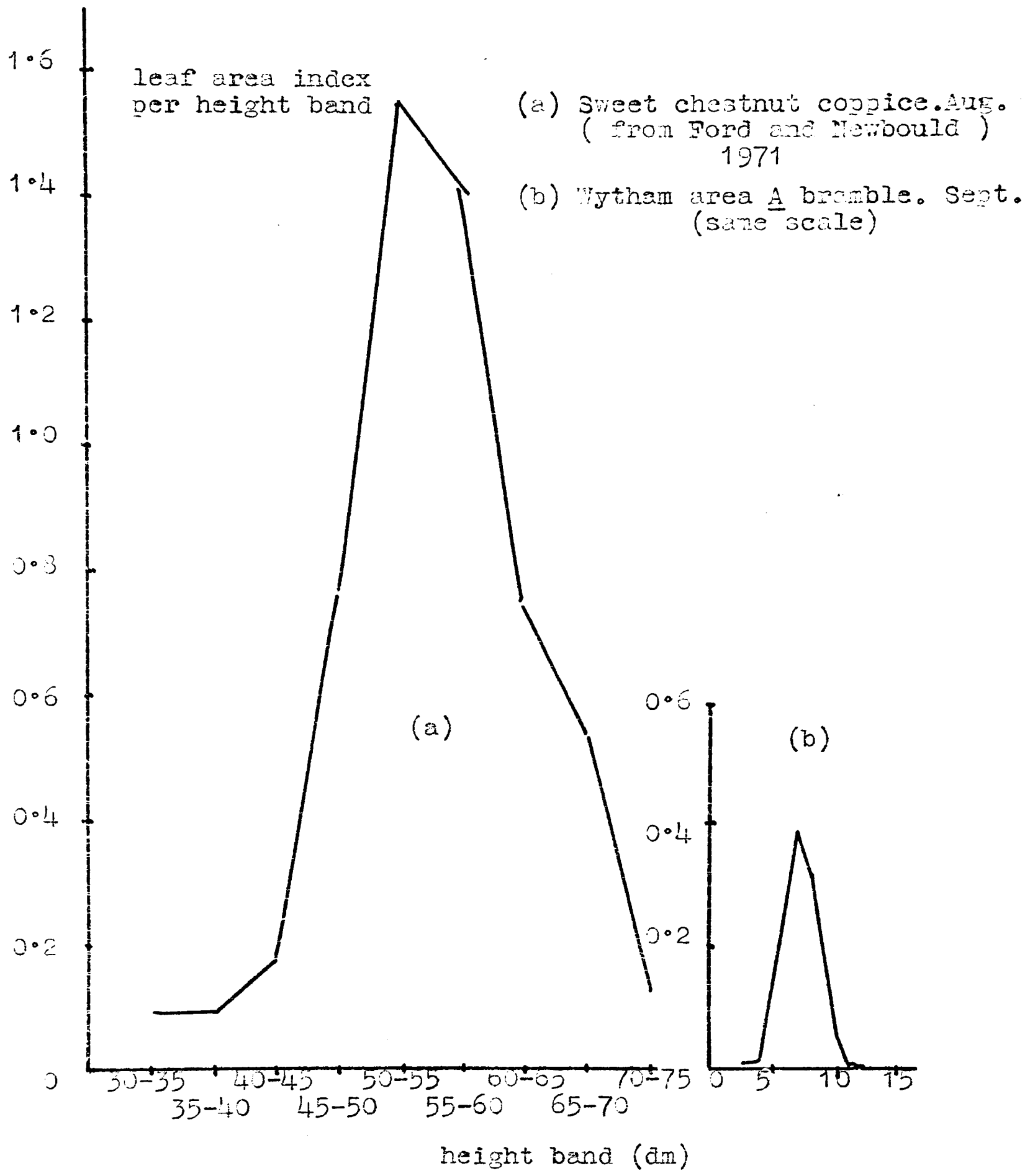


FIG 40



COMPARISON OF BRAMBLE AND SWEET CHESTNUT
CANOPY PROFILES

215. **CHANGES IN PROFILE SHAPE OVER SEASON** Changes in leaf distribution through the canopy were brought about by changes in leaf numbers and by movements of the stems bearing the leaves. Growth of laterals upward raised the height of maximum leaf hits by 10cm during the summer, in A and B. Die-back of laterals from the tip reduced modal leaf height in the autumn. Over the winter the leaves in the upper part of the canopy appeared to be mainly cane leaves.

216. In C laterals were shorter relative to the width of the height bands, The rise in modal height during the early summer was not as pronounced. Because of the low density of stems in C there was less support of stems by inter-lacing with others. In late summer therefore second-year canes settled under their own weight and that of the first-year canes which had grown through the laterals by this time. This caused a downward shift of leaves with very little change in leaf numbers.

STAND STRUCTURE

217. From the canopy profiles and other observations it was clear that, although growth of an individual cane was more or less independent of the canes around it, the interlacing of stems formed a quite-well-ordered structure. This structure, determined by the timing and pattern of stem growth was most apparent in dense bramble stands, such as A, where three layers could be distinguished.

218. **UPPER, CANOPY LAYER** The upper layer contained the bulk of the current-year's canopy. During early summer the laterals, which grew nearly vertically, formed most of this zone. Later in the year first-year canes grew through the lateral canopy and sometimes projected beyond it for a while. The weight of further growth finally caused the first-year

canes to lie more nearly horizontal.

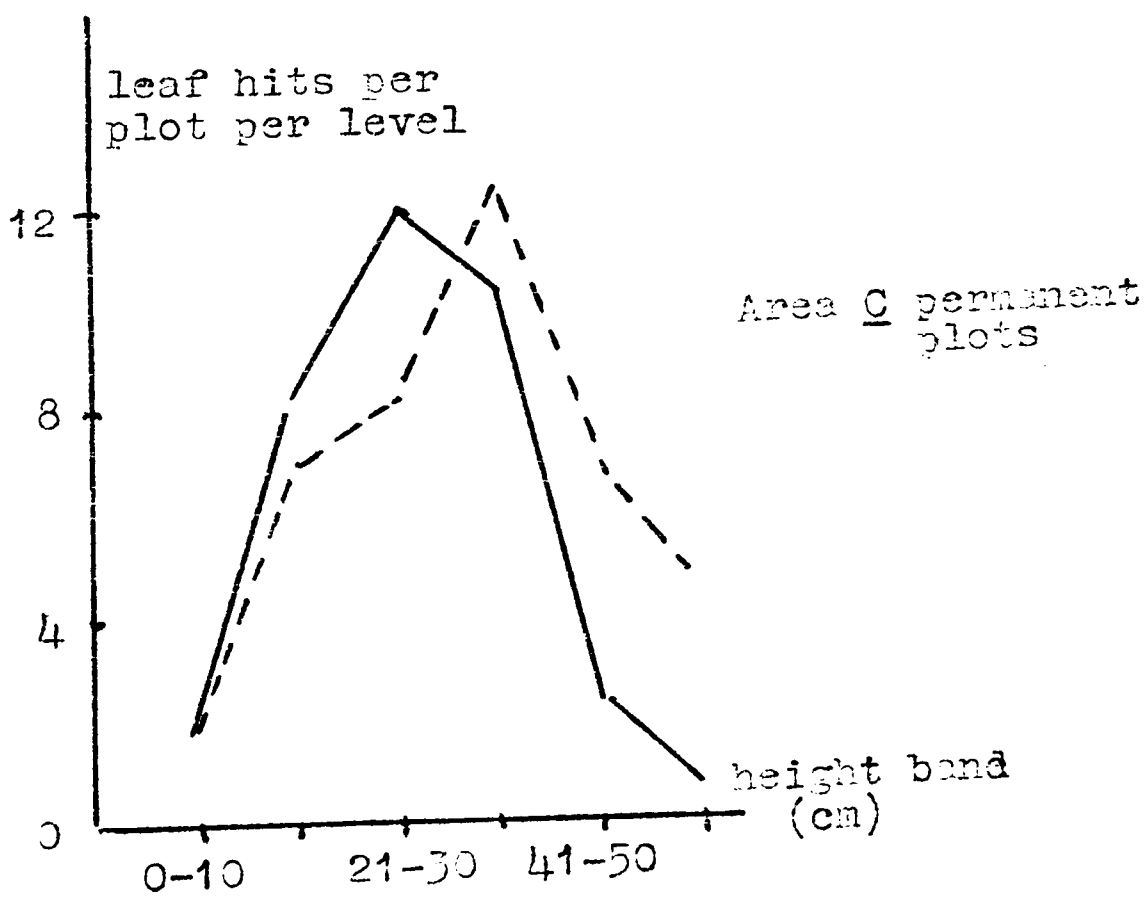
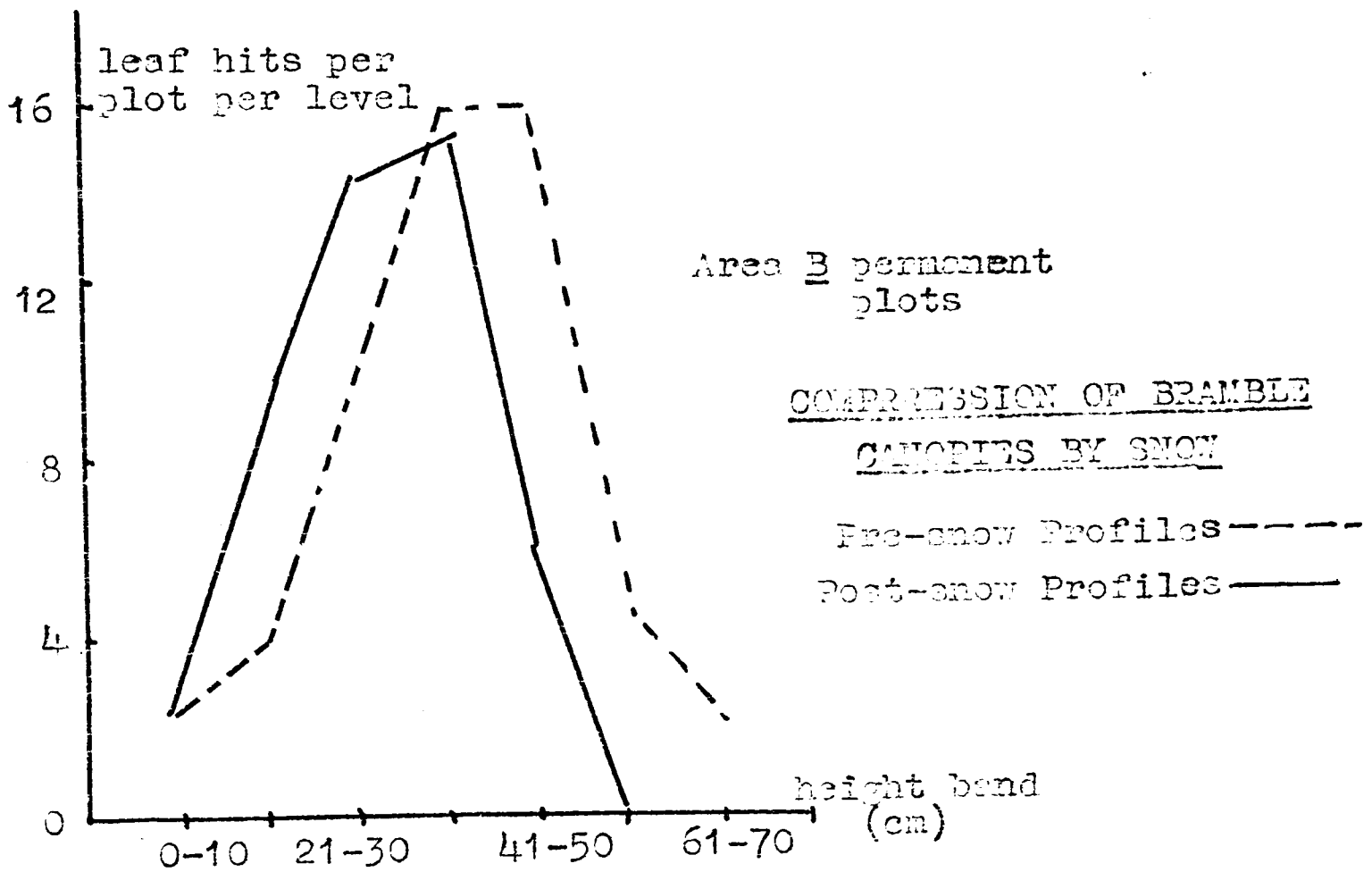
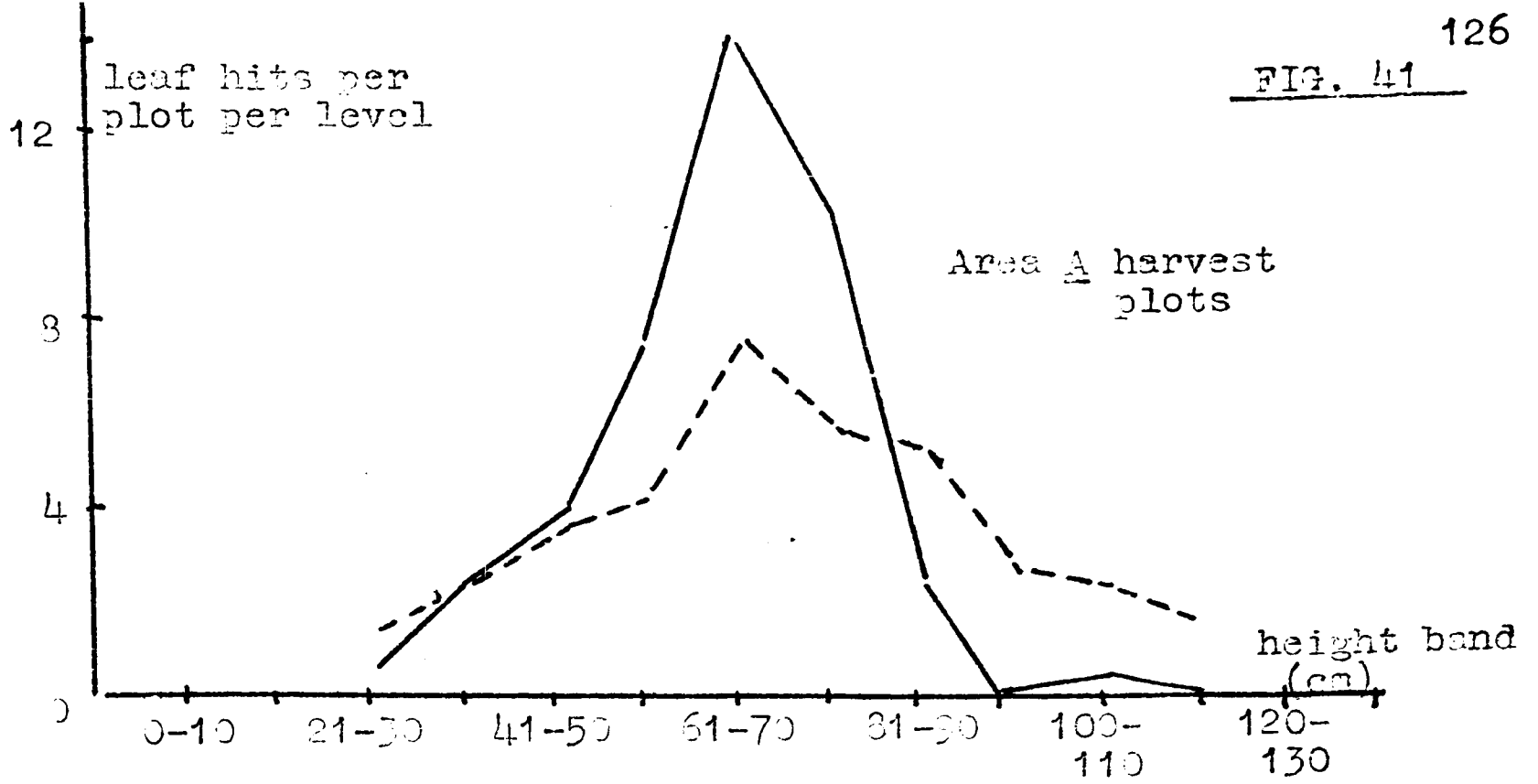
219. **SECOND-YEAR CANE LAYER** The middle zone contained the previous year's canes, also nearly horizontal. Most of the laterals originated in this zone. During the early part of the year it contained the remains of the previous year's laterals and leaves. Growth of new laterals upward ensured that the new leaf canopy was always formed above the old.

220. **LEAFLESS LAYER** At the bottom of the stand was a nearly leafless zone. The sections of first and second-year canes in this layer were predominantly vertical. There were few leaves, because the lowest cane leaves tended to be lost early in the season, while few laterals develop from the lowest buds on a cane. The region also contained the bulk of the standing dead. Accumulation of dead material in the lower part of a bramble stand was also noted by Amor (1971). In certain circumstances this would become a fire hazard. The structure of a bramble stand may also trap wind-blown litter of other species.

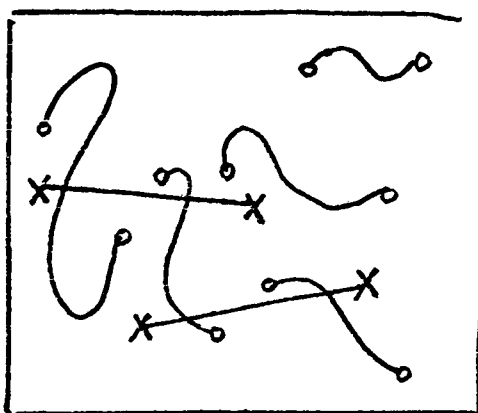
221. Each year's new canes tended to compress the canes and laterals beneath them as they settled under the weight of their own laterals. Gradually each year's canes moved down through the stand. In C the density of plants over much of the area was, however, too low for this type of structure to be fully developed. It existed round clumps of rootstock, which were separated by less dense areas crossed by only a few canes.

222. **COMPRESSION OF A BRAMBLE STAND BY HEAVY SNOW** A sudden downward shift in the bramble canopy occurred after heavy snow on March 14, 1974. The weight of the snow compressed the whole stand structure and was

FIG. 41

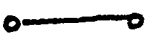


THE INTERSECTION VALUE RELATIONSHIP



If the two sets of lines are distributed at random relative to each other, then the number of intersections between them is given by:-

$$n = \frac{2 \cdot h \cdot r}{a \pi}$$

where h = length of 

r = " " 

a = the given area containing these lines.

or

$$r = \frac{n \cdot a \cdot \pi}{2 \cdot h}$$

For the bramble plots $a = 1 \text{ sq.m.}$

$h = 10 \text{ m}$ (10 lines/plot, each a metre)

$$\begin{aligned} r &= \text{bramble stem-length/plot} \\ &= 0.157 n \end{aligned}$$

reflected in the canopy profiles(^{P.126} Figure 41). Although some loss of leaf occurred, the main change was a result of movement of stems.

INTERSECTION VALUES

223. Stem hits showed no correlation with either stem weight or length per plot because the effective horizontal area of stems was low. Even in area A the number of stem hits per plot was small. An alternative method of stem assessment was therefore devised.

METHOD

224. Buffon (1777) first determined the relation between length of a line within a known area and the number of intersections with a known length of sample line(^{P.127} Figure 42). Newman (1966) used this relation for root length determination, while Loetsch (1973) describes its use for road and canal measurement. The method was used as a basis for estimating stem length in a bramble plot, being tested first in Bagley Wood, and subsequently on the harvest plots in A, B and C in Wytham.

225. INTERSECTION VALUE DETERMINATION Apparent intersections were counted between bramble stems in a metre-square and a metre bamboo rod placed across the plot. This was repeated to give a total of 10 lines/plot. The lines were spread evenly across the plot in two sets of five, at right angles to each other. The numbers of intersections for each line were added to give the Intersection Value (I.V.) for that plot.

226. Where bramble growth was not too dense and tall it was possible to look down on to the rod to count intersections. With larger growth it was necessary to look from one side. Another rod placed vertically at

the far end of the first helped determine which intersections were within the plot and which not. Because the rod had a finite width (6-10mm) there might have been some over-estimation of intersections relative to the theoretical number expected from use of a line. For comparative purposes, however, this did not matter.

227. ARRANGEMENT OF LINES Random positioning and length of sample line was used in root length determination by Newman (1966). Systematic sampling was used here because it made it easier to position the rod and tell exactly where it began and ended. The grid arrangement of sample lines reduced the risk of under estimation where the bramble stems ran largely in one direction or were concentrated in one part of the plot.

228. INCLUSION OF STANDING DEAD It was not possible to distinguish the different types of stem when intersections were counted, so that standing dead was included. Its inclusion reduced the sensitivity of I.V. for detecting growth, which involved changes in the live stem-components only, particularly where standing dead formed a large part of the bulk of a bramble stand.

RESULTS

229. CORRELATION WITH STEM-LENGTH Correlation between total stem length per plot and I.V. was good, $r^2 = 0.73$ (^{P.130} Figure 43). Measured stem length for a given I.V. was greater than that predicted from the formula in ^{P.127} Figure 42 however. This was because effective horizontal length of stem determined the number of intersections, not absolute length. A developing lateral, growing nearly vertically, had fewer intersections per unit length than an old cane which was nearly horizontal. The taller the stand the higher the proportion of vertical sections of stem. Also

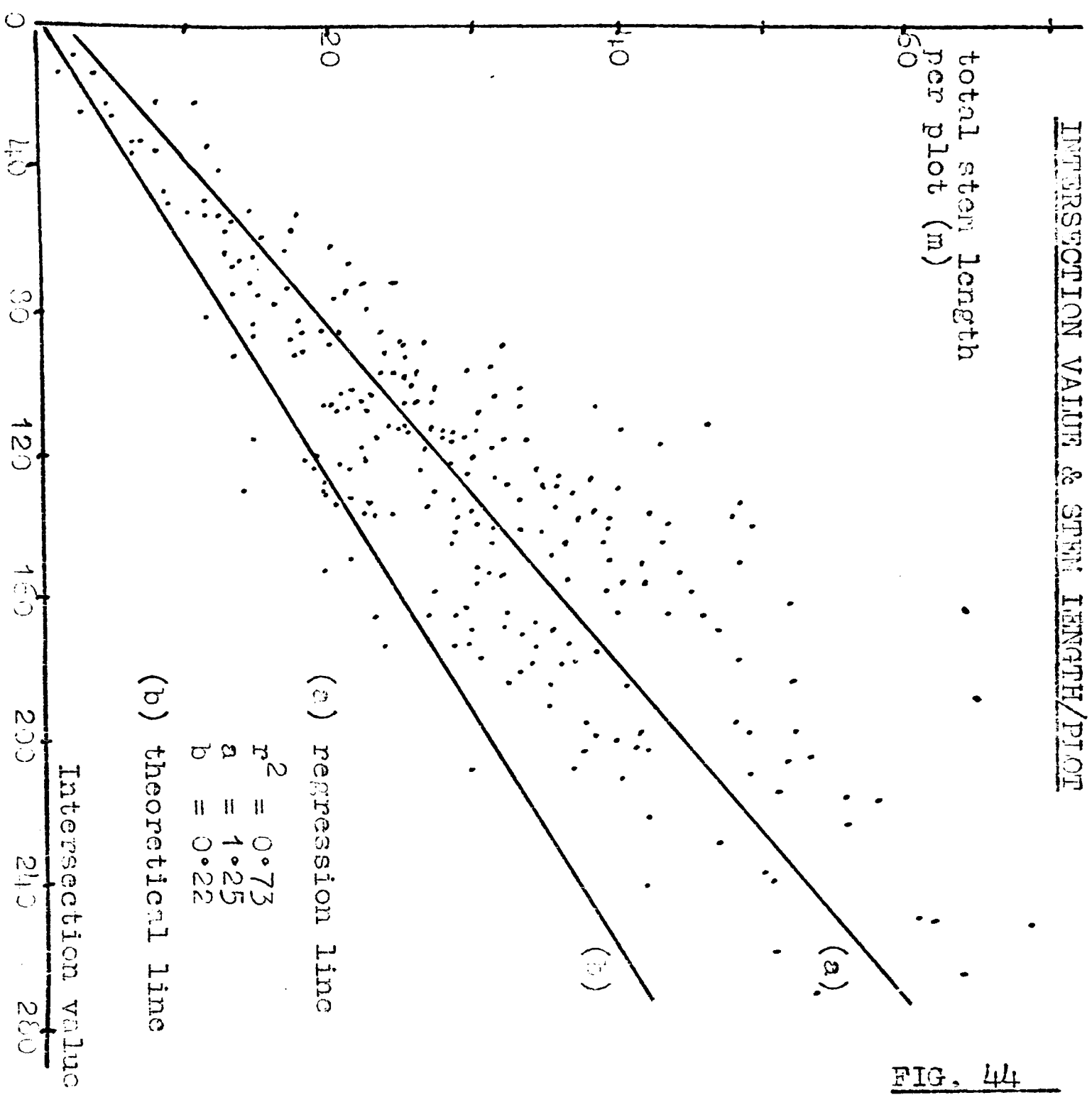
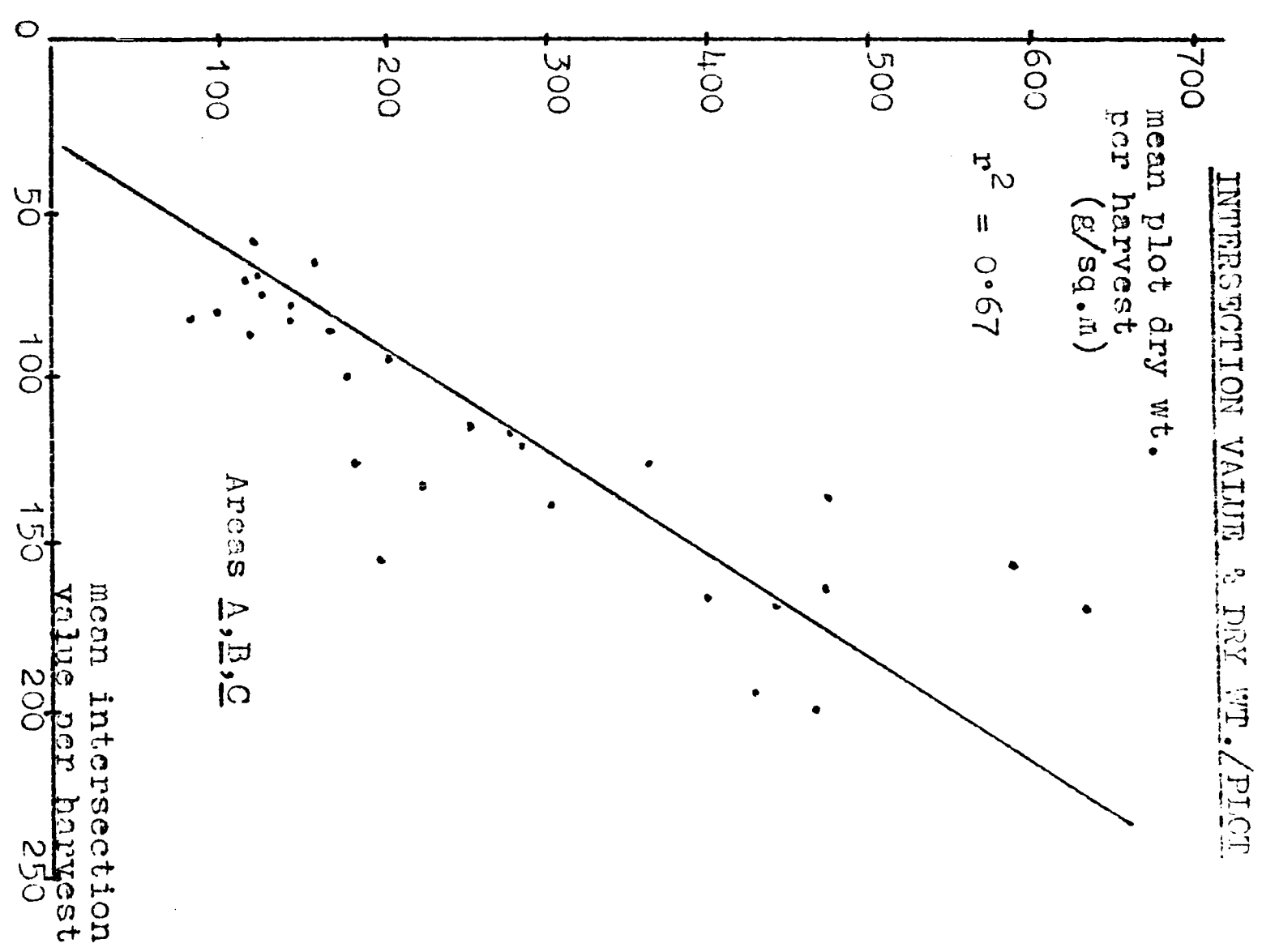


FIG. 44



at high lengths of stem per plot it became more difficult to count all intersections.

230. CORRELATION WITH DRY WEIGHT Stem weights and indirectly leaf weights are related to stem length. Intersection values by themselves, however, were not very useful as estimates of plot dry weight(^{P.130} Figure 44). Differences in stem diameter between area A and the others were partly responsible. The linearity of the relation was improved by multiplying the results for A by a diameter factor to allow for this difference ^{P.132} (Figure 45). The scatter was not improved as no single diameter factor could allow for all the variations between stem components as well as variations during the growing season.

(ADJUSTED INTERSECTION VALUE)

231. INTERSECTION VALUE X HEIGHT CORRECTION Introduction of a height factor was considered as a means of improving the relation between dry weight per plot and intersection values. The height of a bramble stand increased with increasing vigour of growth. Lateral growth, which made very little contribution to I.V., also increased the height of the stand.

232. Mean leaf-height derived from the point quadrat data was chosen as an objective value that was easy to calculate. The use of the zone of most leaf hits, modal height, was considered because it might be less sensitive to small numbers of leaves being lost from the extremes of the canopy. The modal height, however, had a more restricted set of values, changing in sudden jumps, and required more work to find. The changes in mean leaf height, increasing in summer, decreasing in winter, correspond roughly with the changes in total dry weight.

234. REGRESSIONS OF DRY-WEIGHT ON A.I.V. ^{*} Regressions of total dry

^{*} A.I.V. = Adjusted Intersection Value

FIG. 45

MEAN PLOT DRY WT./HARVEST &
INTERSECTION VALUES X DIAMETER CORRECTION

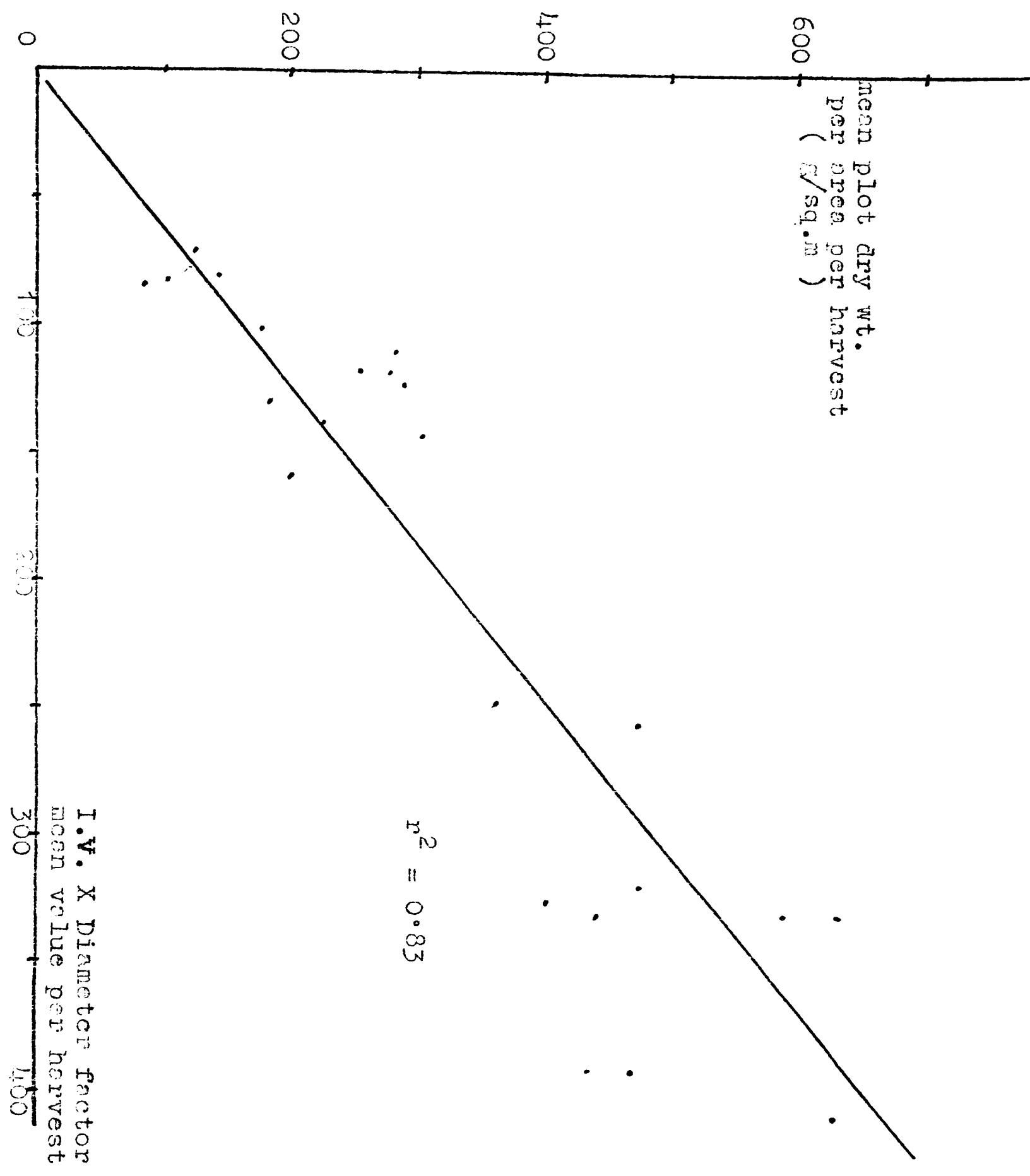


TABLE 37

MEAN CANOPY HEIGHTS BEFORE
AND AFTER A SNOWFALL

Table 37

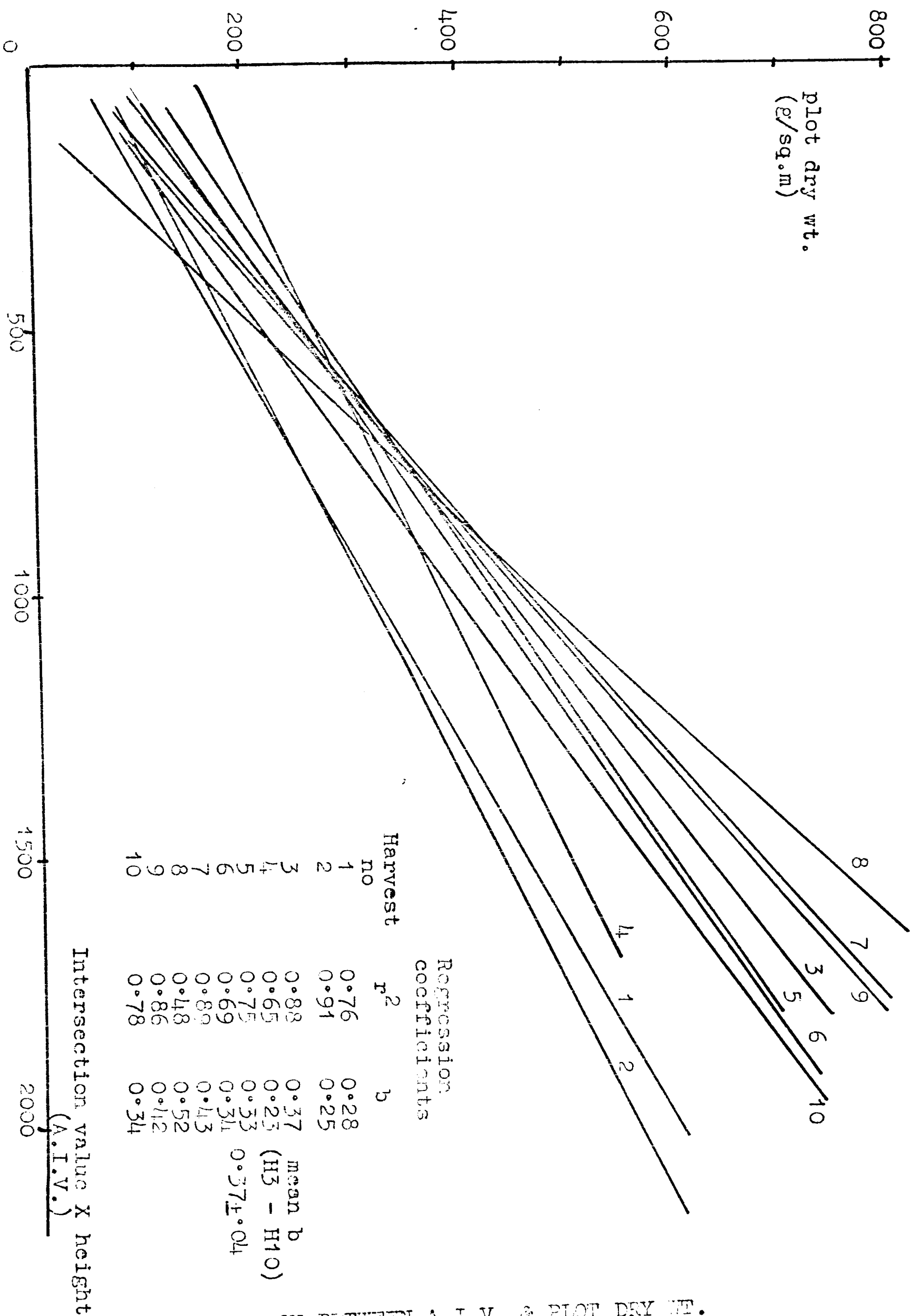
Area	Harvest 1	Harvest 2	Harvest 3	
A	67	79	59	cm
B	36	32	23	"
C	27	31	28	"

The snowfall occurred on Mar. 14th 1974, between Harvests 2 & 3.

weight per plot on Intersection Value X Mean height were calculated for each of the harvests separately (^{P.135} Figure 46). There was no significant difference in the value of "b", the slope, for harvests 3, 5, 6, 7, 9, and 10, but differences in slope were significant between these six "core" lines and those for harvests 4 and 8. These two harvests appeared to be extreme values of the same relation as the other harvests and had the lowest values of r^2 , 0.65 and 0.48 respectively. ^{P.136} Figure 47 shows a regression based on all the individual plot data for harvests 3-10, while ^{P.137} Figure 48 is based on mean values per area for each harvest.

235. ANOMALY OF HARVESTS 1 AND 2 The lines for harvests 1 and 2 were quite distinct from the rest, as was the regression for the two combined, ^{P.136} (Figure 47). The discrepancy appeared to be mainly caused by the values from area A (^{P.137} Figure 48). Intersection values for H. 1 and 2 were not very different from those of subsequent harvests, rather there was a reduction in mean canopy height between harvest 2 and harvest 3 (^{P.133} Table 37). This was caused by the snowfall of March 14, 1974 mentioned on page 125. If the height values of H. 3 are used with the intersection values of harvests 1 and 2, the results for these harvests are brought into line with those of the other harvests (^{P.137} Figure 48).

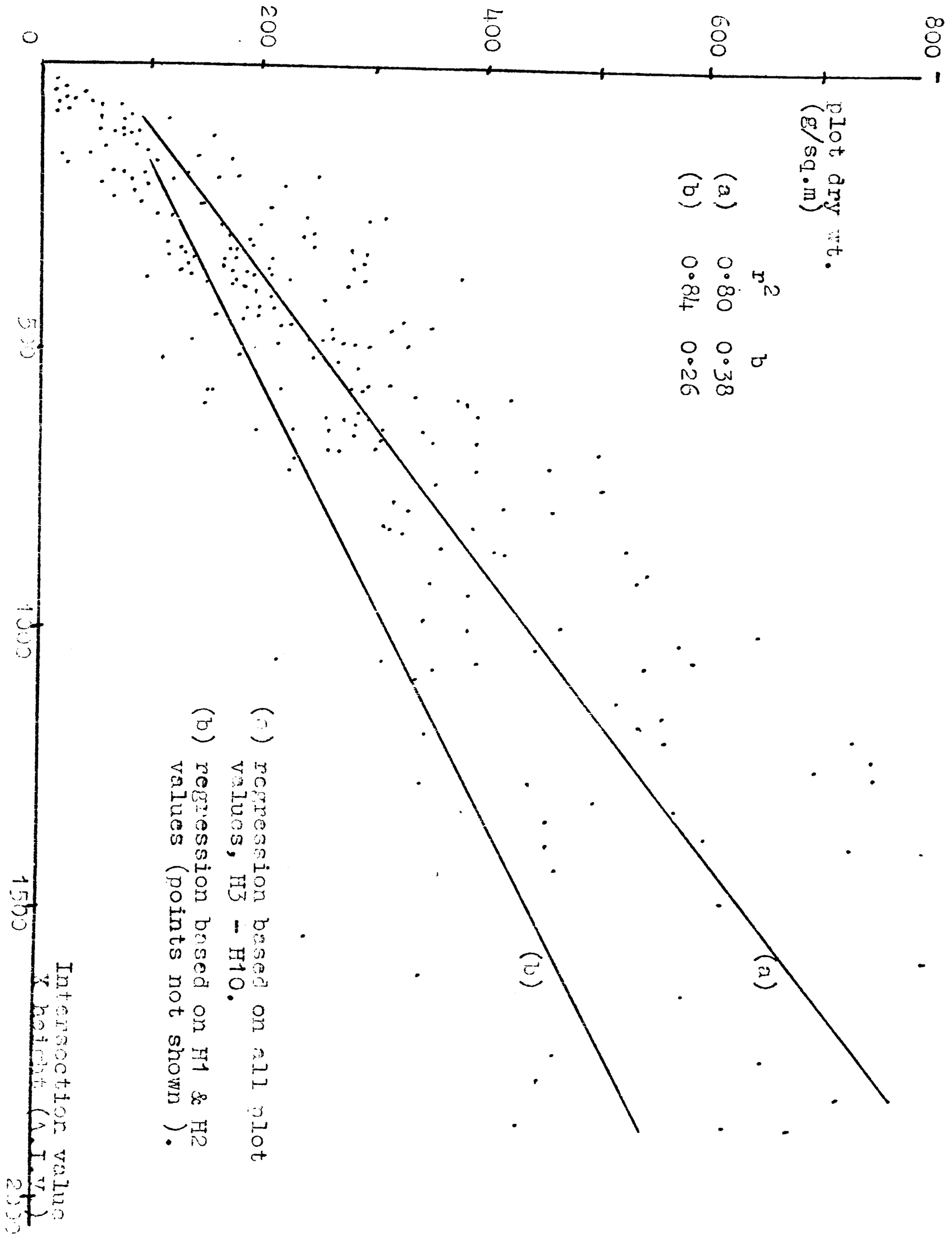
236. Thus while intersection values x mean height (A.I.V.) allowed for the gradual settling of cane which occurred during the winter months, it gave inaccurate results where any sudden drastic change happened. No similar such change was detected in either of the winters, 1974/75, 1975/76. Although such changes, when they occur, prevent comparisons between recordings made at different times, they do not affect comparisons between areas recorded at the same time.



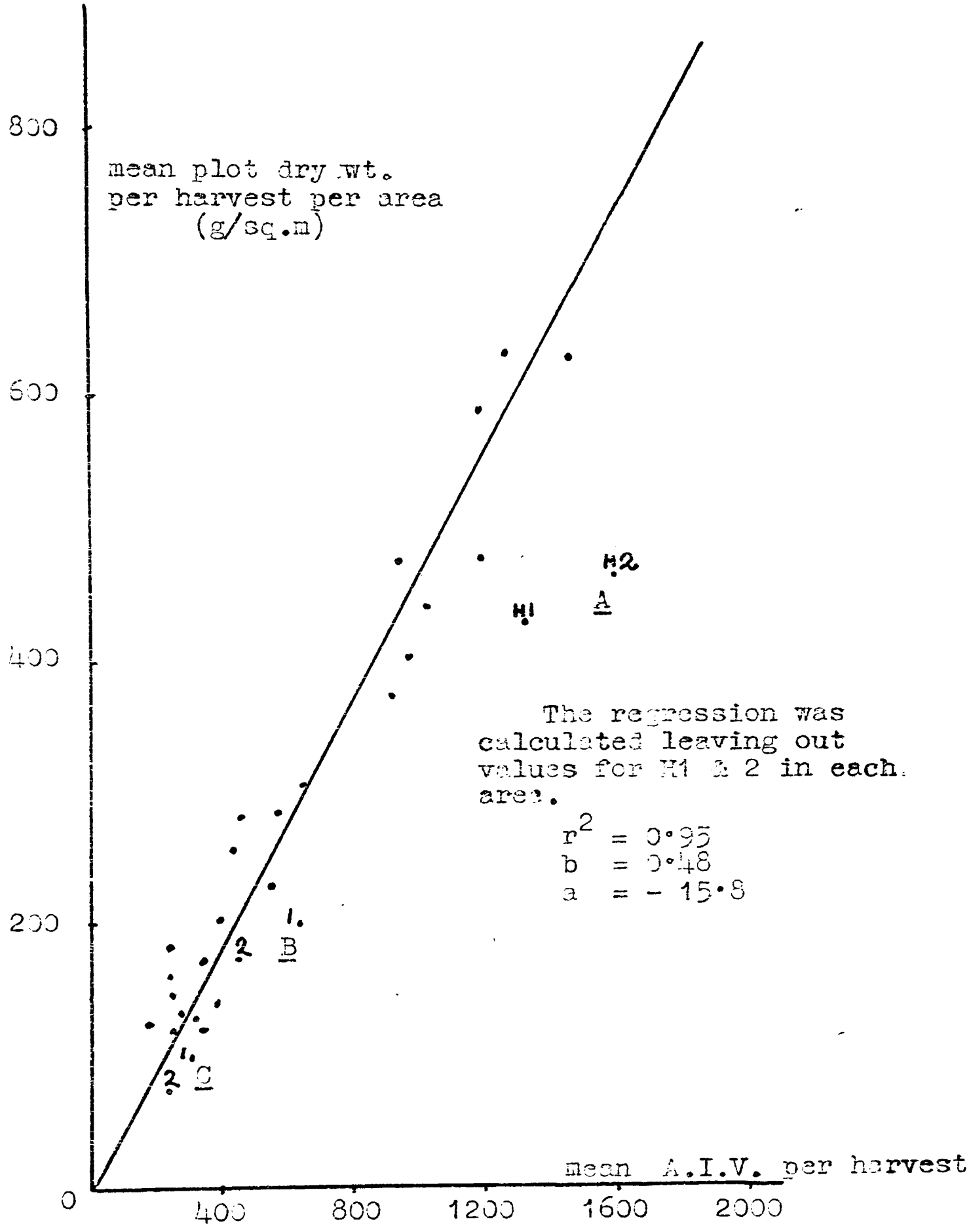
RELATION BETWEEN A.I.V. & PLOT DRY WT.
FOR EACH HARVEST

FIG . 47

RELATION BETWEEN A.I.V. & PLOT DRY WT.
HARVESTS COMBINED



MEAN VALUES FOR EACH HARVEST OF A.I.V.
AND PLOT DRY WT.



P.139

237. CONCLUSIONS ON USE OF A.I.V. Figure 49 shows the results of Figure 48 in a different way. The curves for total dry weight per plot and A.I.V. are superimposed. These show that A.I.V. is a useful measure for comparing the dry weight of plots from different parts of the wood. It is applicable over a wide range of bramble growth, though its precision declines above A.I.V. = 1500. Subsequent sections include its use to measure growth in other areas of the wood.

A.I.V. CHANGES IN THE PERMANENT PLOTS 1974-76

P.140

238. A.I.V. curves for the permanent plots are shown in Figure 50, B combines the results from all 5 plots. The curve for A excludes plot 5 whose A.I.V. in winter was 1800, beyond the limit of usefulness. Plots 1 and 2 in C are shown separately from the others because of the unusual die-back that occurred in them (P.141 Figure 51).

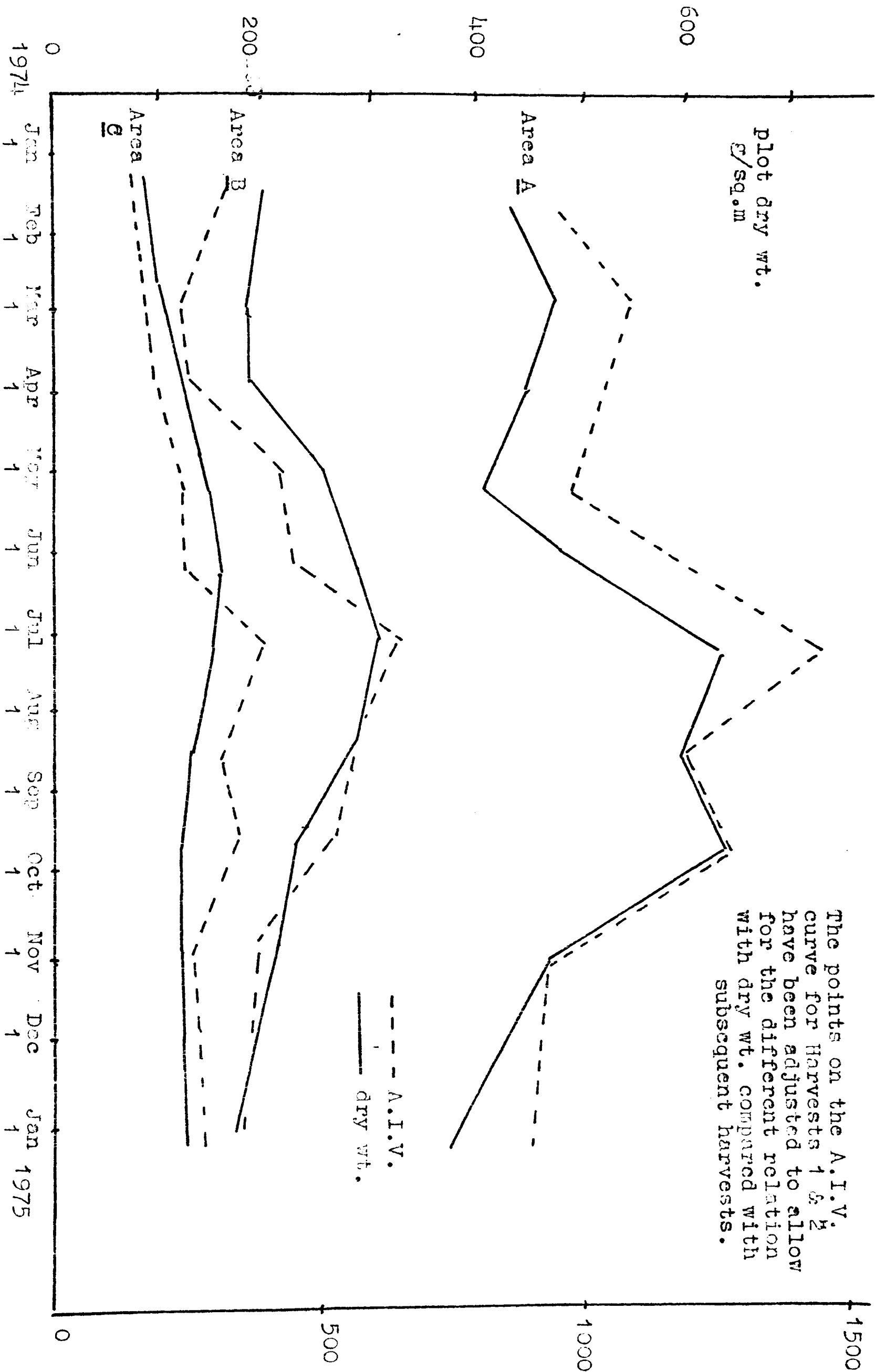
239. As was found for leaf hit values, mean A.I.V. for the permanent plots in A and B was greater than those for the harvest plots. The permanent plots were sited, subjectively, in areas "typical" of growth in A and B. There was a tendency to avoid places where the cover was not quite continuous i.e. to site the plots in areas where growth was greater than, rather than less than, the average for the area as a whole.

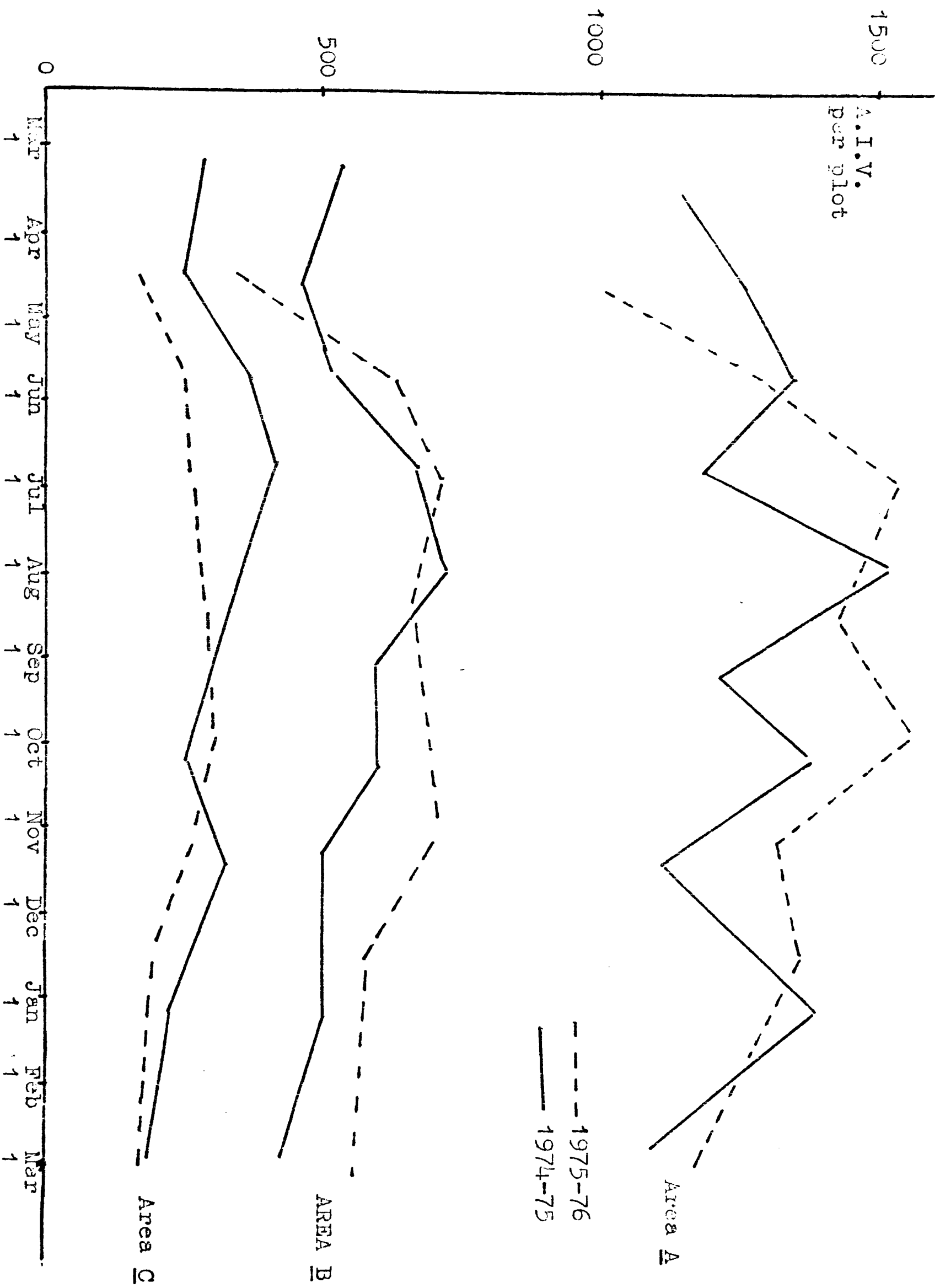
240. FIRST RECORDING OF B AND C The first recording of the permanent plots in B and C took place before the snowfall of March 14th. The A.I.V.s were thus higher than expected compared with subsequent recordings because of the compression of the bramble and change in the A.I.V.-dry weight relation.

241. LINEAR AND QUADRATIC EFFECTS FOR A.I.V. CURVES The significance of the linear and quadratic tendencies for the different curves was tested

FIG. 49

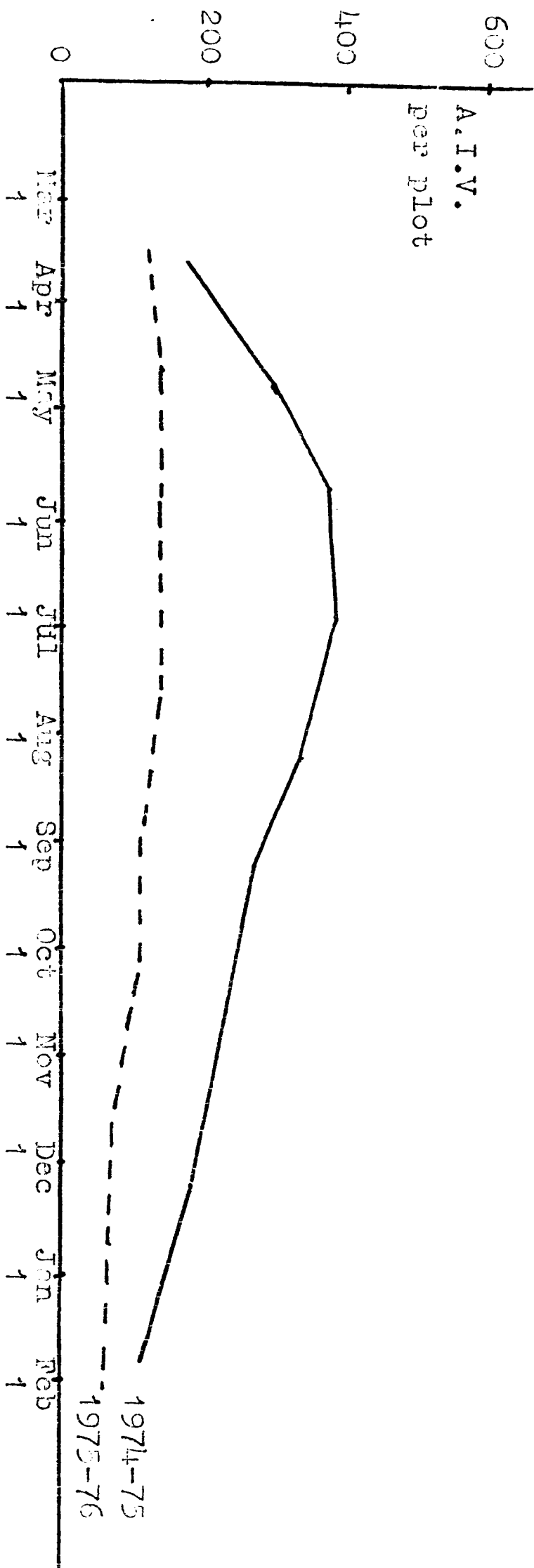
A.I.V. & DRY WT. CURVES OVER THE SEASON





A.I.V. CURVES FOR PERMANENT PLOTS IN 1974-1975, 1975-1976

FIG. 51



A.I.V. CURVES FOR PERMANENT PLOTS 1 & 2 IN AREA C

by response curve analysis. (Snedecor 1967). The quadratic effect in this case represents the summer peak, corresponding to the peak in biomass. This was significant for all six curves on Figure 50. ^{P.140} Linear trends represent changes in the mean level of bramble biomass present between different years.

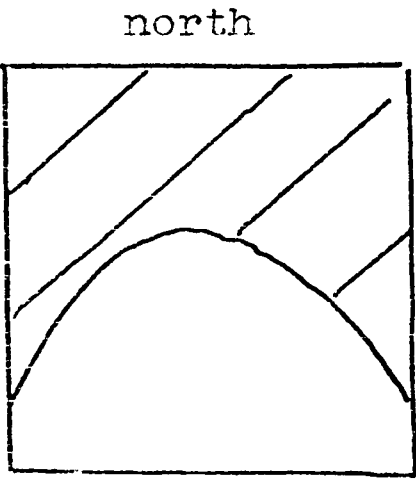
242. YEAR-TO-YEAR DIFFERENCES Differences between the curves for different years may be caused by random year-to-year fluctuations in growth about a mean level, e.g. those caused by the weather. Alternatively there may be a definite trend to the differences between years. This could be long-term, as when a site is being invaded or bramble is gradually dying out from an area. Trends in mean dry weight might also be short-term and cyclical as has been found for a number of species. (Watt 1947).

243. A showed no linear trend over the two years, suggesting that the level of dry weight in the plots was relatively stable. The summer peak in 1974 was however irregular compared to that for 1975, or to the peak shown in the harvest plots. It is not known why this was so. B had a significant upward trend for A.I.V. in 1975, while C (plots 3,4,5) showed a significant downward trend in 1974. As the areas were only studied for 2 years it is not possible to say whether these trends continued or were random year-to-year differences.

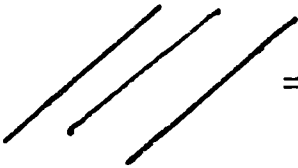
244. CYCLICAL CHANGES Cyclical changes in bramble growth at a point could lead to a mosaic of different stages in the cycle of an area. If it existed the permanent plots in an area were unlikely to be all at the same point in this cycle. The ranking of the plots in terms of dry weight per unit area might thus change in different years. Although

CHANGE IN THE DISTRIBUTION OF BRAMBLE WITHIN A PLOT
BETWEEN YEARS

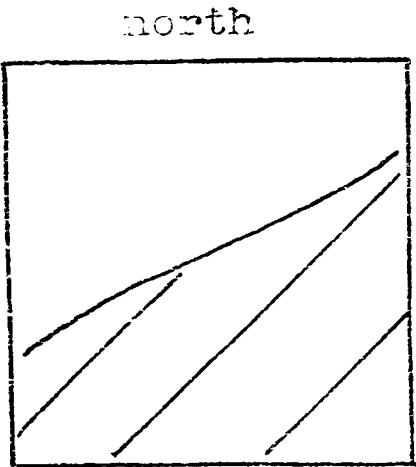
Area B - permanent plot 2.



1974



= approximate distribution
of winter leaf cover.



1975

significant differences existed between plots over the two years, there was no evidence for a change in the relation between plots during this time. However, as canes live for at least two years a longer period would probably be necessary to detect any cyclical change of the sort envisaged.

245. RANDOM FLUCTUATIONS IN BRAMBLE GROWTH WITHIN A PLOT In an area of low density bramble, the dry weight of bramble contained within a plot, in a given year, may depend a lot on the orientation of individual canes. If a cane grows such that the bulk of it falls outside the plot then the biomass is much lower than in another year when the growth of the cane falls within the plot. The effect will be particularly noticeable during the second-year of the cane's life, as flowering canes provide the bulk of the biomass over the year. ^{P.143} Figure 52 illustrates this sort of variation for a permanent plot in B. In areas of higher stem density, overall plot dry weight depends less on the individual cane, while the greater stand structure allows for less possible movement of the canes.

SOURCES OF CARBOHYDRATES FOR GROWTH IN BRAMBLE

INTRODUCTION

246. The carbon requirements for growth in a year may be met either from current photosynthesis or from reserves laid down at a previous time. The contribution of reserves for a plant growing from a seed is usually small. For established plants reserves in the perennating organs are larger and transfer growth plays a greater role. With perennials any drain on the reserves must be restored by current photosynthesis if long term growth is to be maintained. With biennials this does not happen to any great extent as the whole plant usually dies after two years. Where growth is transfer based, the level reached in a given year may depend as much on the previous years' conditions, where the reserves were laid down, as on the current growing season.

247. **TRANSFER GROWTH IN BRAMBLE** Two clear opportunities for transfer growth in bramble are (1) growth of first-year canes on root reserves, (2) growth of the laterals on cane reserves. More complicated patterns of transfer are not ruled out, but seem less likely. Both canes and laterals bear leaves, so that while early growth in each case may depend on reserves, later growth could be based on current photosynthesis. At some stage during the life of a cane any drains on the root reserves must be restored. This could occur during the first-year, or take place at the end of the second year, perhaps by withdrawal of material during die-back of canes and laterals.

DEFOLIATION EXPERIMENTS - METHODS

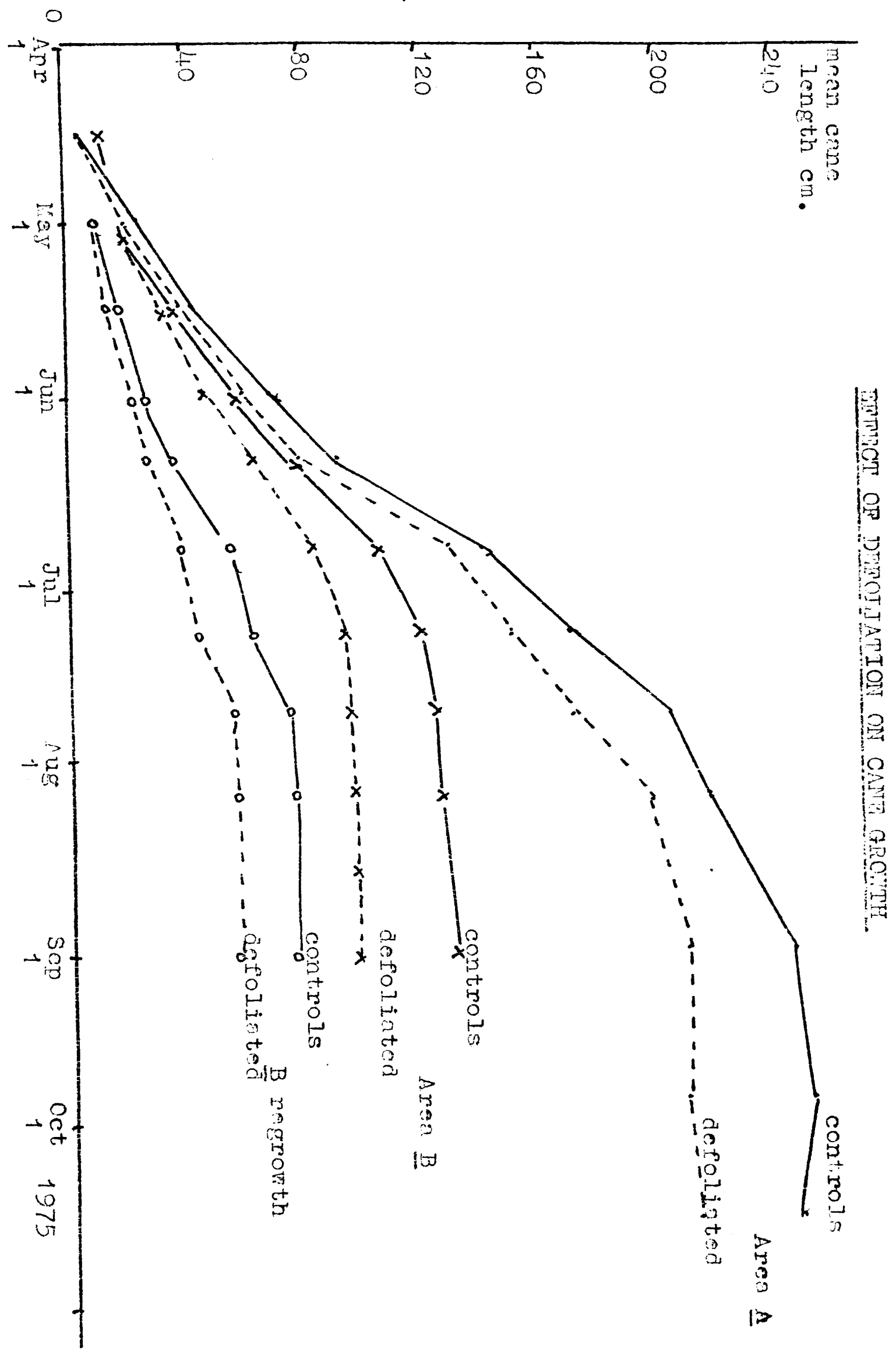
248. Leaves were removed, as they formed, from developing laterals and first-year canes, to try to investigate the relative contributions of transfers and current photosynthesis to overall growth. The experiment started in spring 1975 when canes had just emerged from the litter. The canes were not more than 15cm long and the leaves not separate from the growing point. The laterals were up to 3cm long with at most one leaf 25% expanded.

249. During the growing season stems were checked at least once a week and new leaves removed as soon as this could be done without damage to the growing point. Even during the period of most rapid leaf expansion, there was seldom more than one partially expanded leaf to be removed per stem. Measurements of stem length were made at 2-3 weeks intervals. Stem diameters and internode numbers were also recorded.

250. **STEMS AND AREAS USED** Eight first-year canes were selected for defoliation in areas A and D. Fifteen were marked in Area B with another 10 in a regrowth area, cleared of bramble in autumn 1974. The same number of canes were marked in each area as controls. A third group of canes were marked, and had their leaves removed in late August, when extension growth was virtually complete.

251. Five second-year canes were marked in A and D, ten in B for removal of lateral leaves as they formed, with a similar number as controls. In 1976 the growth of laterals on the canes defoliated in 1975 was measured. Half the canes in each treatment had their laterals

FIG 53



EFFECT OF DEFOLIATION ON CANE GROWTH

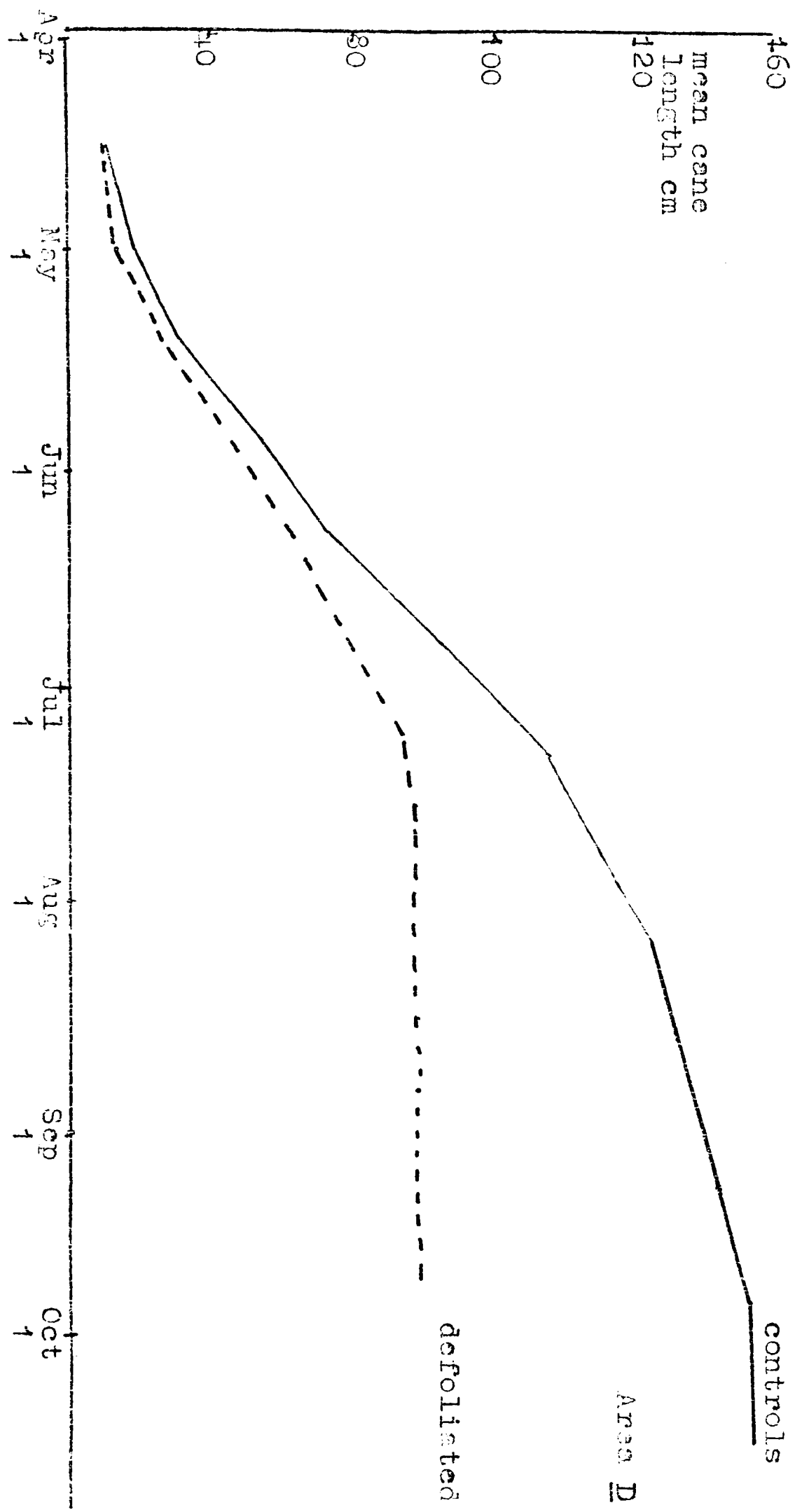


TABLE 38

NO'S OF NODES ON DEFOLIATED
AND CONTROL CANES

Table 38

Area	Controls	Leaves removed in autumn	Leaves removed as they formed
A	32.1 ±1.5	35.5 ±2.9	31.7 ±3.1
B	17.1 ±1.4	19.8 ±1.4	17.3 ±1.2
B regrowth	10.7 ±0.8	12.3 ±1.7	12.3 ±1.2
D	21.7 ±2.6	23.5 ±3.3	16.6 ±1.4

TABLE 39

DEATH OF DEFOLIATED 1st YEAR CANES

Table 39

Area	No of canes per treatment	No dead Autumn leaf removal	No dead Leaves removed as they formed
A	8		2
B	15	2	7
B regrowth	10	1	3
D	8		1

TABLE 40

DIAMETERS OF DEFOLIATED 1st YEAR CANES

Table 40

Area	Controls	Autumn leaf removal	Leaves removed as they formed	
A	9.6 ±0.5	9.8 ±0.3	10.3 ±0.2	mm
B	6.9 ±0.3	6.7 ±0.3	6.2 ±0.2	"
B regrowth	4.2 ±0.3	4.3 ±0.3	4.2 ±0.3	"
D	4.6 ±0.5	4.7 ±0.2	4.7 ±0.4	"

defoliated also.

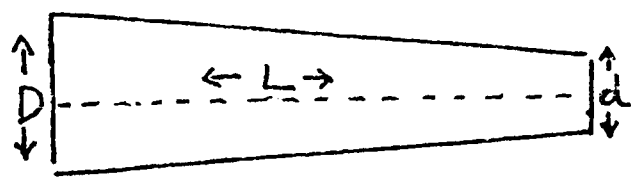
RESULTS - CANE GROWTH

252. Defoliation reduced the final length of the canes(^{P.147,148} Figure 53). This was mainly a result of reduction in internode length(^{P.149} Table 38) rather than a reduction in numbers of nodes. Defoliation also caused some canes to die in their first year(^{P.149} Table 39). There were no differences in stem diameters between defoliated and control canes (^{P.149} Table 40). Removing the leaves in the autumn from the cane did not have any immediate apparent effect.

253. PHOTOSYNTHETIC CAPACITY OF DEFOLIATED CANES Removal of the leaves greatly reduced the photosynthetic capacity of the defoliated canes. There is very little net export of carbohydrate from a leaf during the early stages of its expansion, (Thrower 1962) so that the contribution of the leaves before they were removed must have been small. Stem photosynthesis can occur in bramble. The area of stem surface was, however, less than 15% that of the leaves on the control canes(^{P.151} Table 41). The stem is less well-adapted for photosynthesis and much of its length is shaded by being in the lower part of the stand. Thus it seems unlikely that stem photosynthesis made much of a contribution to the growth requirements of the defoliated cane. The bulk of its growth was thus presumably based on rootstock reserves.

254. SIZE OF ROOT RESERVES Rootstocks in A were larger than those in B and probably contained greater reserves. Reserves in the regrowth area were probably reduced as a result of the removal of the shoot system the

TABLE 41



If the stem tapers uniformly , the surface area is

$\frac{1}{2}\pi L(D + d)$

If the angle of taper is small, L = the cane length.

Stem surface area (defoliated canes)		Leaf-area/cane (controls)	<u>Stem area</u> leaf area
	sq.cm	sq.cm	
Area <u>A</u>	514	3986	0.13
<u>B</u>	143	2164	0.07
<u>B</u> regrowth	53	1268	0.04
<u>D</u>	104	2850	0.04

TABLE 42

ROOTSTOCK SIZE AND GROWTH BY
DEFOLIATED CANES

Table 42

Area	Defoliated cane length as % control length	Weight of root crown (mean of 6 plants)
A	86	36.3 g
B	79	6.7 "
B regrowth	69	-
D	50	0.7 "

TABLE 43

REDUCTION OF FLOWERING ON
DEFOLIATED LATERALS (1975).

Table 43

Area	Mean lateral length	% of laterals flowering
A control	50 cm	76
B "	35 "	68
A defoliated	29 "	64
B "	15 "	22
D control	12 "	0
D defoliated	7 "	0

previous autumn. The proportion of cane growth apparently supported by root reserves declined from A - B regrowth(^{P.152} Table 42), The reduction in growth of defoliated canes relative to the controls was greatest in area D which had the smallest rootstocks. The difference in length between defoliated and control canes was exaggerated in this area, however, because most of the controls tip-rooted, while only one of the defoliated canes did so.

255. **AUXIN PRODUCTION** The reduction in length growth by defoliated canes might have been partly caused by lower auxin levels as a result of removal of the younger leaves. The youngest leaves, however, those immediately around the growing point, were not removed. There was also no increase in the number of lateral branches formed in the first year which should have accompanied any reduction in auxin levels.

256. **DEATH OF DEFOLIATED FIRST-YEAR CANES** Death of defoliated canes in the first-year was greater than that of the controls. Other canes on the same rootstock were not affected, which suggests exhaustion of respiratory substrate in the cane itself may have been responsible. Death of canes appeared to be most prevalent in area B, but there was no apparent reason for this.

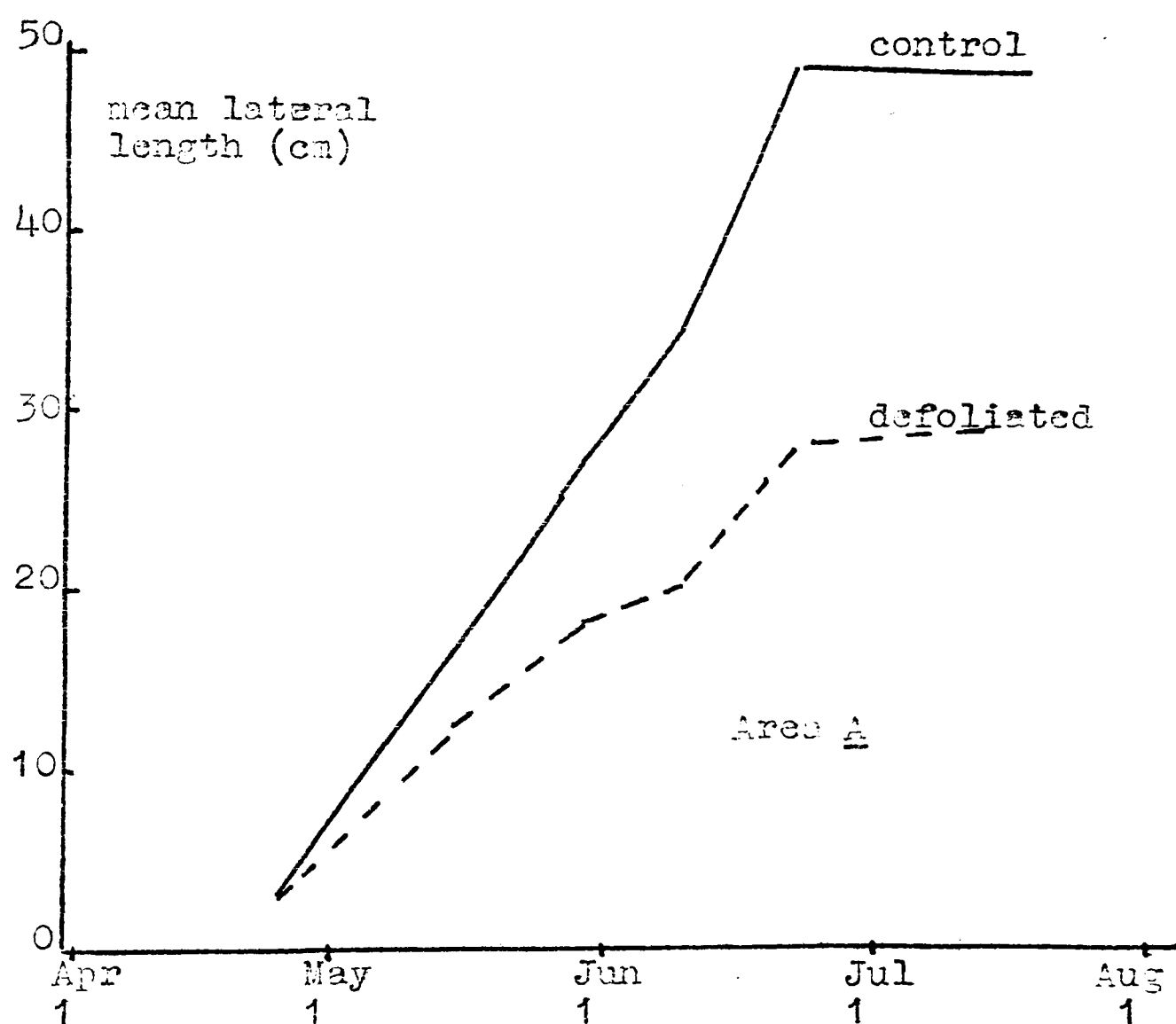
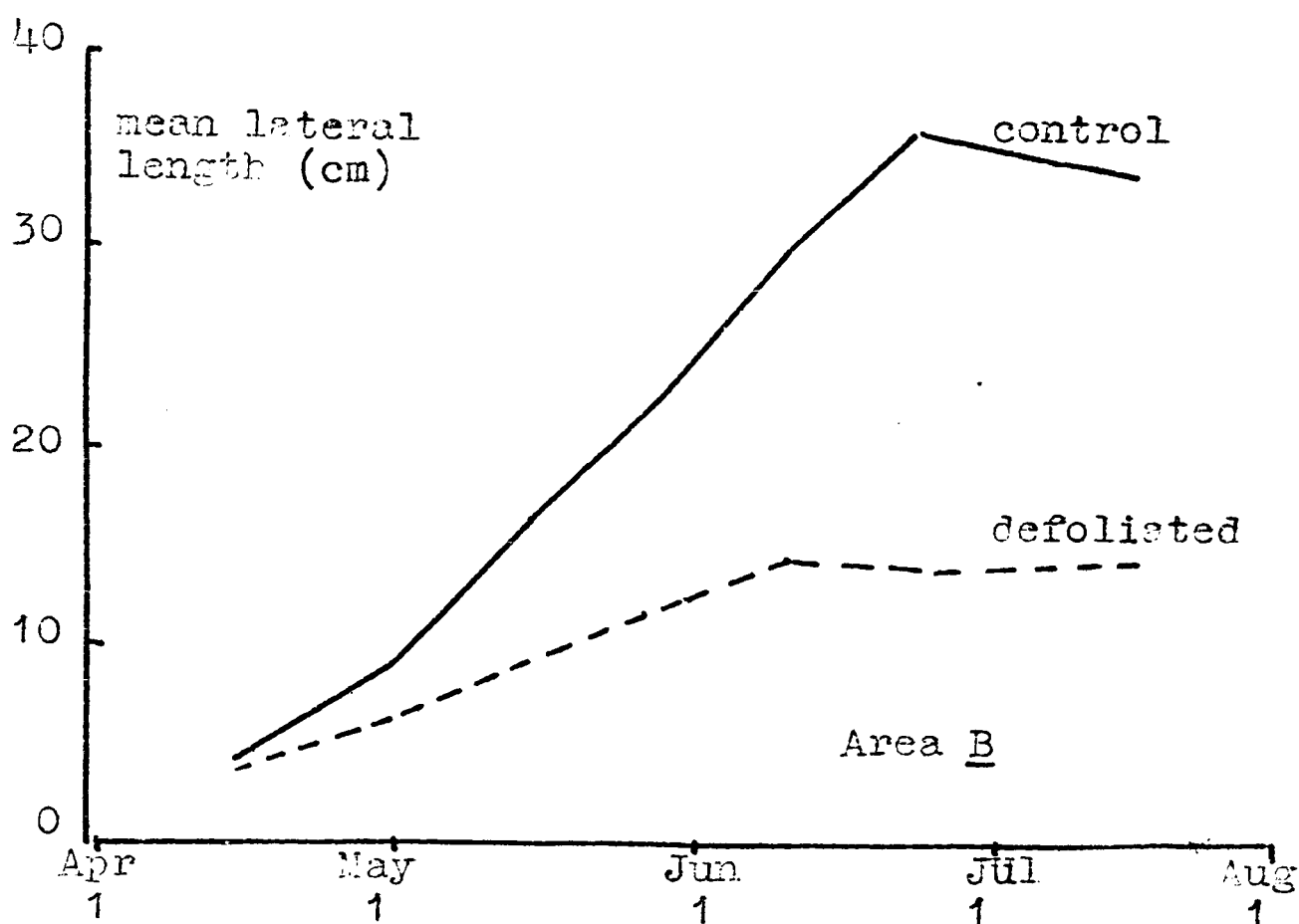
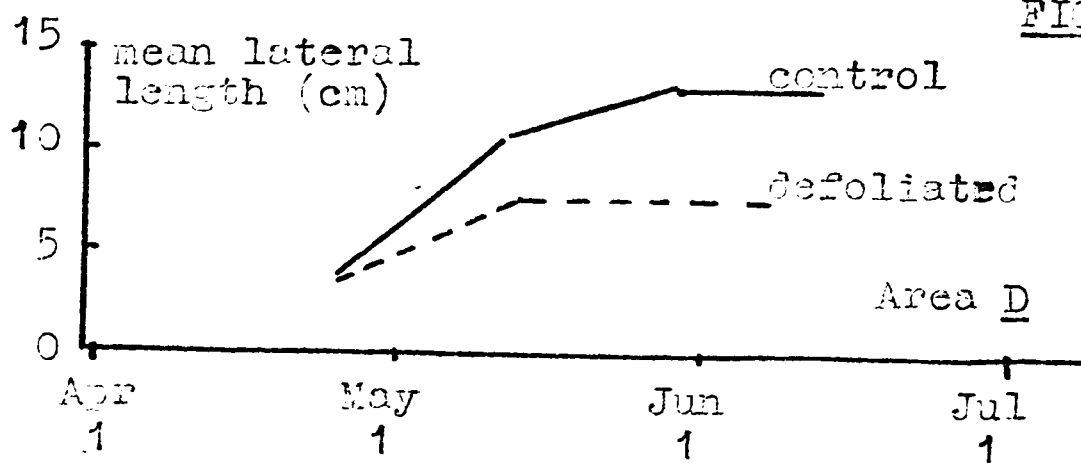
257. **SIGNIFICANCE OF TRANSFER GROWTH IN FIRST-YEAR CANES** The first-year cane often grows below a continuous canopy of bramble lateral leaves for much of the time, as well as ^{under} the fully developed tree canopy. It is only when cane growth is nearly complete and the lateral leaves die off that many of the cane leaves reach a position in the canopy favourable for photosynthesis. A high degree of growth based on reserves is thus necessary for first-year canes.

LATERAL GROWTH

258. DEFOLIATION OF LATERALS THEMSELVES The reductions of lateral length caused by defoliating the laterals themselves are shown in Figure 54. ^{P.155} Initially the numbers of laterals in the defoliated and control treatments were the same. In A, however, the weakening of the ⁱprimary lateral growth by defoliation led to some of the secondary buds developing. As with the canes, the reductions in length were caused by shorter internodes rather than by fewer nodes. Flowering was reduced on the defoliated laterals, along with their reduction in length(^{P.152} Table 43).

259. GROWTH OF LATERALS ON CANES DEFOLIATED IN 1975 Growth of laterals in 1976 for the different treatments are shown in Table 44. ^{P.156} Variability between canes in the uncleared bramble in B was very high and no significant differences were found for the various treatments. For the other areas, there was little difference between lateral growth on canes defoliated in autumn and those defoliated from the start of growth. Both treatments resulted in less lateral growth than on the control canes. Defoliating the laterals themselves reduced their growth as in the 1975 measurements.

260. DISCUSSION The drop in weight of second-year canes during growth of the laterals, found by Sykes and Taylor (In press) and also seen in Wytham B, is evidence for transfer of material from canes to laterals. If the same assumptions about stem photosynthesis are made as for cane growth then these measurements indicate that up to about 50% of lateral growth could be supported by cane reserves. This was less than the transfer contribution to cane growth. Since the lateral leaves form the bulk of the bramble canopy up until flowering, during part of which time there is only



GROWTH OF DEFOLIATED LATERALS

an incomplete tree canopy, a greater contribution by direct photosynthesis to lateral growth might be expected.

261. A, which had the greatest diameter canes, showed the highest apparent reserve growth compared to the controls, but that in D was greater than B. The errors in measurement of laterals were greater relative to the final length in D and a greater proportion of length growth had already occurred when the experiment started.

262. The similarity of 76 lateral growth on the two cane defoliation treatments shows that some of the reserves on which lateral growth was based were laid down in the autumn or over winter. The reduction in reserve growth was not subsequently made up by increased direct growth. Some lateral growth occurred even where no mature leaves were formed either on the first-year cane or the laterals. This may represent the products of stem photosynthesis or transfers from the root.

CONCLUSIONS ON TRANSFER GROWTH IN BRAMBLE

263. These results indicate that unless stem photosynthesis is a much larger quantity than assumed here, from 50-90% of first-year cane growth can be supported by root reserves. This explains the strong regrowth that occurs after an area has been cleared of bramble. Growth of laterals depends more on direct photosynthesis than cane growth does. Its partial dependence on cane reserves means, that vigour of lateral growth is directly related to that of first-year canes. Laterals may however show a greater response than canes to environmental change, in the year in which the change occurs. There is evidence that photosynthesis by cane leaves from September onwards is important in determining first-year cane reserves, and subsequent lateral growth.

REGROWTH OF BRAMBLE

INTRODUCTION

264. The capacity for regrowth that is shown by bramble is an important factor in maintaining its abundance on many sites. In woodlands considerable damage maybe done to the plant during thinning, logging, etc. In addition there may be deliberate attempts at controlling bramble by cutting it or spraying it with herbicides. The processes of bramble regrowth were followed in an area from which all top growth had been removed.

265. THE CLEARINGS All bramble stems were cleared away from 100 sq.m of Area B in October 1973 as part of an undergraduate practical. This was repeated on another 100 sq.m in October 1974. The cut material was placed outside the clearings. Some damage may have been done to the rootstocks by the trampling that accompanied the cutting. The regions that were cleared were chosen because their bramble growth was typical of that over the whole of area B.

266. ASSESSMENT OF REGROWTH Measurements of regrowth were made during 1975-76. The area cleared in autumn 1974 was thus in its first-year of regrowth that cleared in autumn 1973 in its second. The surrounding uncleared bramble, which contained the five permanent plots in B acted as a control - the equilibrium state for bramble in that stand which the clearings were expected to regain. Three metre-square plots were set out in the middle of each clearing, to avoid the influence of canes growing in from the surrounding uncleared bramble. These were recorded

TABLE 45

REGROWTH OF CANES AND LATERALS
AFTER BRAMBLE CLEARANCE

Table 45

a) Density of canes

	1st yr. regrowth (9 plots)	controls (5 plots)	
Primocanes no's	7.2 ±1.2	7.8 ±0.9	per sq.m

b) Cane lengths (cm)

	1st yr. regrowth	2nd yr. regrowth	controls
1974	97.9 ±13.1		144 ±23
1975	72.1 ±7.9	123.5 ±13.8	124 ±8.0

	1974	1975
<u>1st yr. regrowth</u>	0.68	0.58
controls		

c) Lateral lengths (cm)

	2nd yr. regrowth	3rd yr. regrowth	controls
1975	26.2 ±3.1		36.5 ±2.8
1976	12.8 ±1.2	25.3 ±0.9	23.4 ±2.0

	1975	1976
<u>1st yr. regrowth</u>	0.72	0.55
controls		

d) Laterals/cane

	2nd yr. regrowth	3rd yr. regrowth	controls
1975	7.3 ±0.6		10.8 ±0.7
1976	5.5 ±0.6	9.6 ±1.0	9.0 ±0.9

in the usual way: leaf hits, I.V., A.I.V.. Individual cane and lateral lengths were also measured.

267. **NATURE OF REGROWTH** In the first year of regrowth only primocanes were present. In the second year laterals were produced, but only in the third year of regrowth were there all the components found in an established bramble plot. Some of the relationships, on which non-destructive measurements of bramble plots are based, may not therefore be strictly applicable to regrowth.

CANE AND LATERAL LENGTHS

268. ^{P.159} Table 45 shows mean lengths of canes and laterals in the different years of regrowth. In the second year of regrowth cane lengths were the same as in the controls. Lateral growth necessarily lagged a year behind cane growth in its recovery. In the third year after clearing both cane and lateral growth were back to the level shown in the uncleared bramble.

269. Following clearing there was no increase in the numbers of first-year canes per unit area. Thus it does not appear that the main buds on the rootstock were damaged by trampling, as this would have led to several axillary buds developing.

REGROWTH PLOTS

270. **LEAF-HITS: FIRST YEAR** Because only cane leaves were present, the number of leaf hits per plot in the first year of regrowth was less than in the permanent plots in the uncleared bramble (^{P.161} Figure 55). The difference was greatest in summer, when the lateral leaves formed the bulk of the control canopy. The decline in leaf-hits in the autumn in

FIG. 55

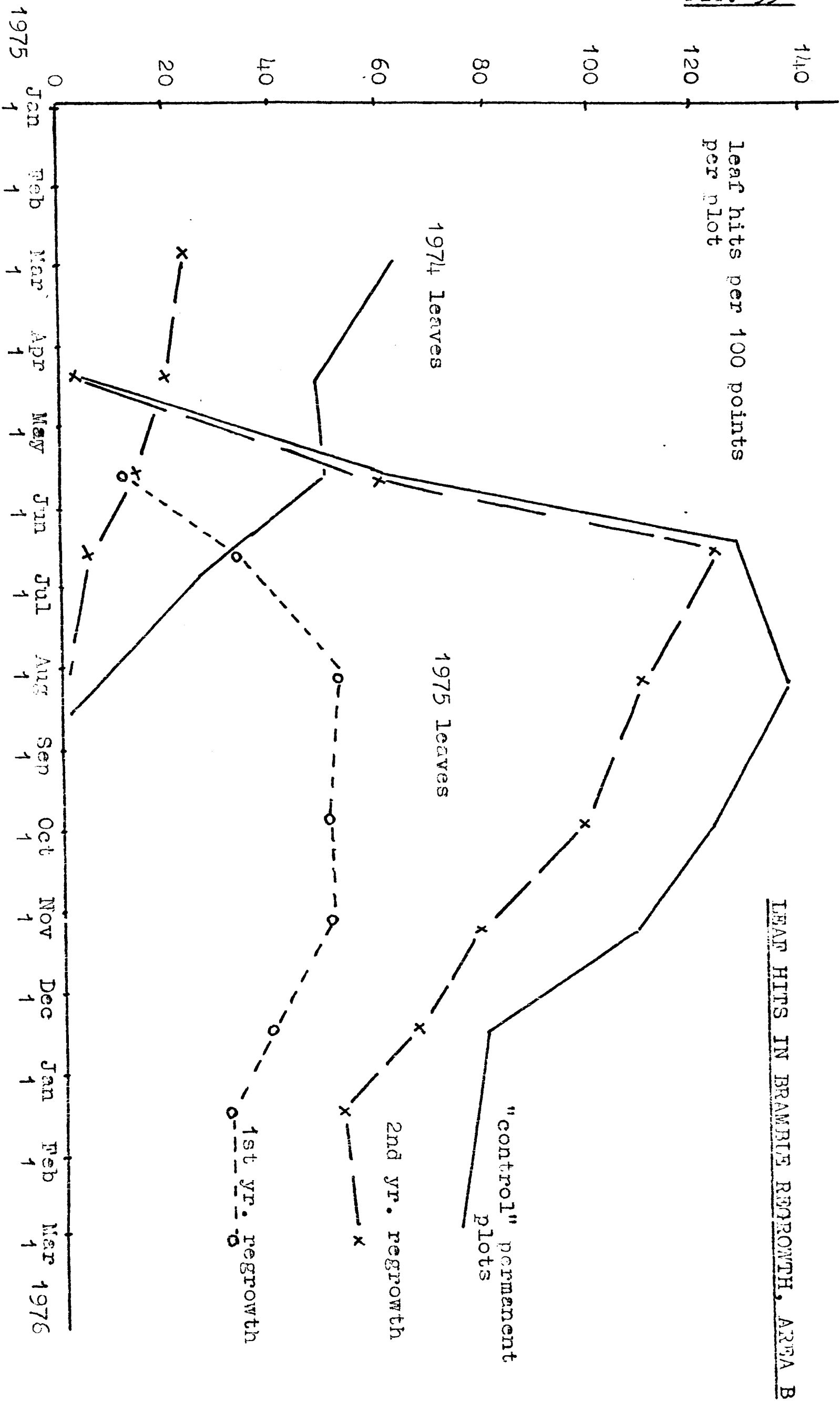


Table 46

EXPECTED LEAF HIT NO. IN FIRST YEAR
OF REGROWTH

Expected no = P x Q x R

where P = no of leaf hits for the control plots (1975)

$$Q = \frac{\text{length of a 1st yr. cane in the regrowth}}{\text{" " " " " " " " controls}}$$

R = cane leaves as a proportion of total leaf
in uncleared bramble (from the Harvest plots).

	Expected no	Observed no.
Sept..1975	42	51 ±6.3
Nov "	45	51 ±12.3
Jan 1976	30	31 ±6.2

Table 47

EXPECTED INTERSECTION VALUES FOR
REGROWTH PLOTS

Estimated length of stem per metre-square, derived from
lengths of individual stems and the density of plants.

1st yr regrowth	5.19 m
2nd yr regrowth summer	28.4 "
" " " winter	22.3 ..

Using these lengths, an expected I.V. can be found from
Fig 47, p.136.

	Expected I.V,	Observed I.V.
1st yr regrowth	18	44 ±2
2nd yr " summer	124	84 ±8
" " winter	98	71 ±4

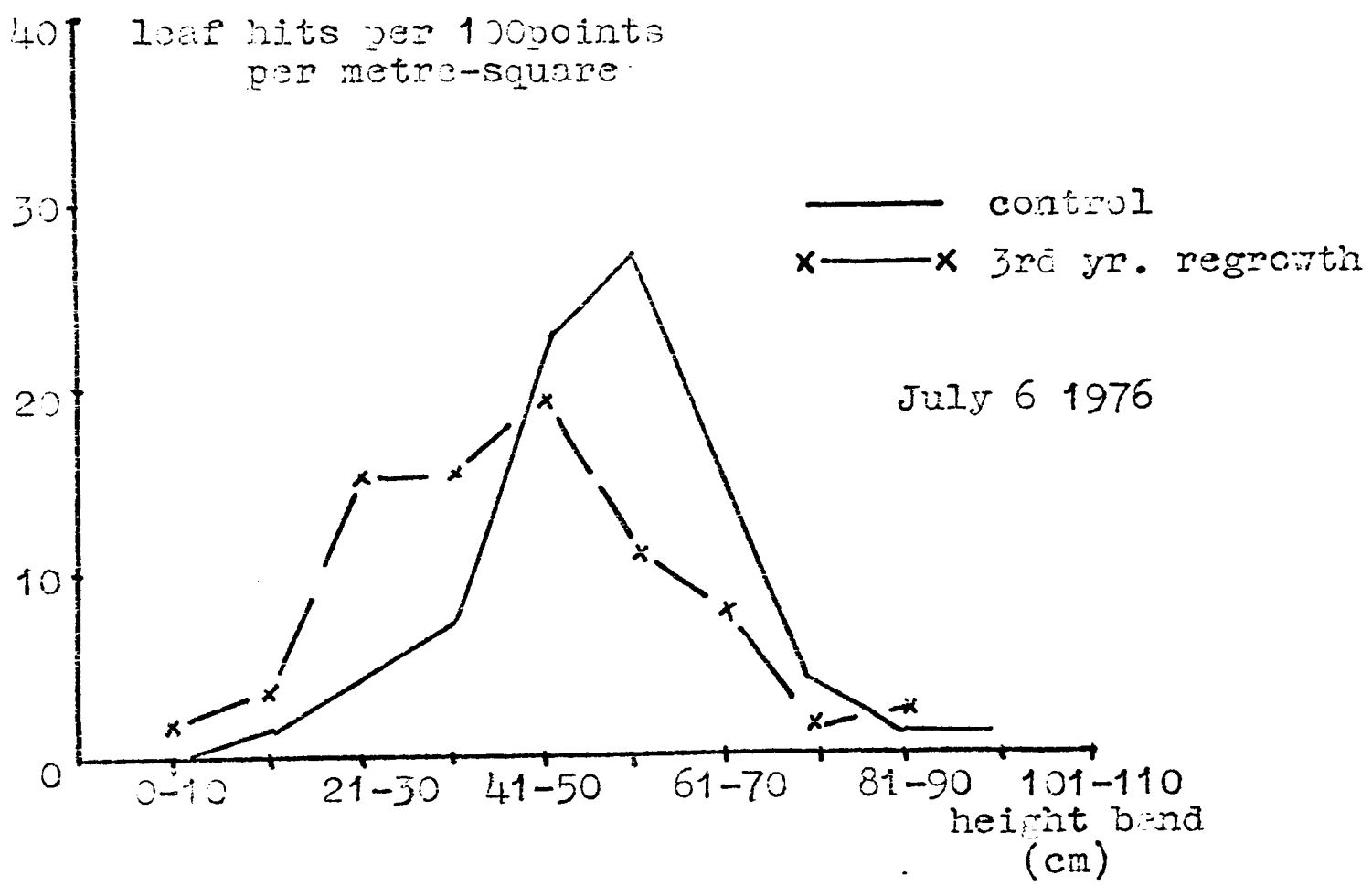
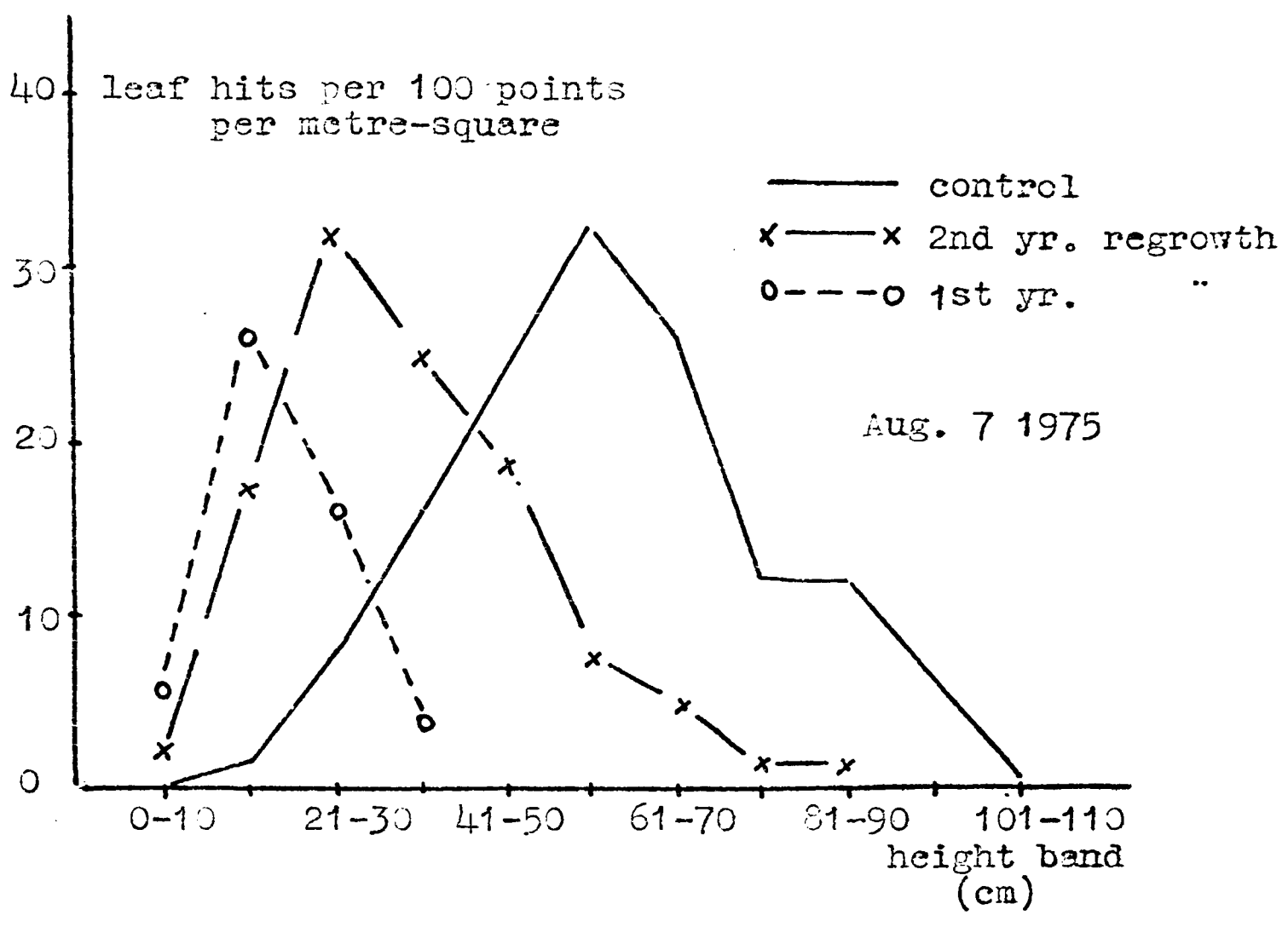
the regrowth was a result of the "settling" of canes and changes in leaf angle rather than any large loss of cane leaves. ^{P.162} Table 46 gives the number of leaf hits expected in the regrowth plots, from various other measurements.

271. LEAF HITS: SECOND YEAR OF REGROWTH Although cane leaf production was the same as controls in the second year of regrowth, the laterals leaf production was reduced relative to the uncleared bramble. Summer leaf hits were less in the regrowth, second year, than in the controls. The reduction relative to the controls was expected to be less in the winter than in the summer because of the greater contribution of cane leaves to the winter canopy. However, this was not so ^{P.161} (Figure 55). It may be that the discrepancy lies with the control plots rather than the regrowth plots as there was a greater winter canopy in the permanent plots 1973-76 than in 1974-75, see page ¹¹⁴.

272. CANOPY STRUCTURE All the older canes that would have provided support for the new growth were removed when the areas were cleared. The new canes in the regrowth, therefore, were more horizontal and inclined to settle under their own weight. In this respect the regrowth resembled parts of area C. ^{P.164} Canopy profiles for regrowth are shown in Figure 56.

273. INTERSECTION VALUES Canes in the first year of regrowth were more horizontal than in the surrounding bramble and so produced more intersections per unit length. Observed values were about twice the expected values ^{P.162} (Table 47). Expected intersection values for the second year of regrowth were relatively closer to the observed values, because the stems were more vertical, the structure was closer to that of the

FIG. 56



CANOPY PROFILES IN BRAMBLE REGROWTH, AREA B

TABLE 48

ESTIMATES OF DRY WEIGHT FOR THE
REGROWTH PLOTS

Table 48

a) Expected values

For each stem component, it is assumed

Dry weight in regrowth plots = $W \times R$

where W = dry weight of that component in the
harvest plots

$R = \frac{\text{length of that component in the regrowth}}{\text{" " " " " " " " controls}}$

The ratio for leaf component weights between regrowth
and controls is assumed to be equal to that for the
stems on which they are borne.

b) Derived dry weights are obtained from Fig. ^{P.136}47 using the
measured A.I.V. for the regrowth plots.

	Expected dry weight	Derived dry weight	
1st yr. regrowth winter	65	82	g/sq.m
2nd " " summer	195	162	"
" " " winter	131	125	"

TABLE 49

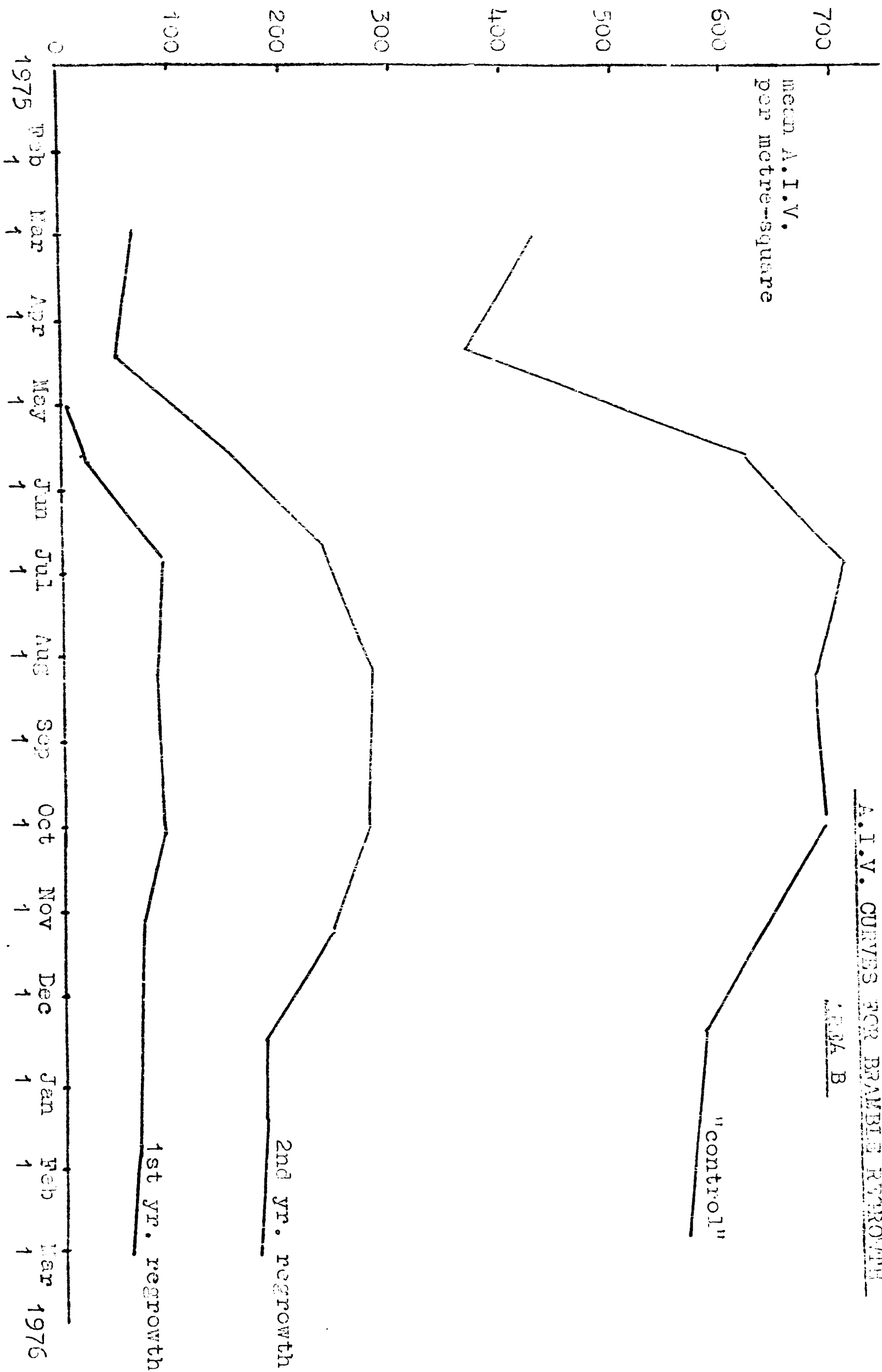
COMPARISON OF 3rd YR. REGROWTH
WITH UNCLEARED BRAMBLE

Table 49

July 6th 1976

	3rd yr. regrowth	Controls	
Leaf hits	81 ± 3	85 ± 12	per sq.m
I.V.	123 ± 5	136 ± 3	"
A.I.V.	518 ± 25	709 ± 48	"
Derived dry weight	256	329	g/sq.m

Fig. 57



controls.

274. ADJUSTED INTERSECTION VALUES (A.I.V.) ^{P.166} Figure 57 shows A.I.V. for the regrowth. ^{P.165} Table 48 compares dry weights derived from A.I.V. curves with expected plot dry weights, based on the components present and the level of growth shown by each in the regrowth relative to the controls.

275. THIRD-YEAR REGROWTH The final recording of the regrowth plots took place in July 1976. The differences between the area cut in 1973, in its third year of regrowth, and the controls were significant but small.

DISCUSSION

276. Within three years of removal of all top growth there was virtually full recovery of the bramble growth, while leaf cover and cane growth were only slightly reduced in the second year relative to the controls. The bramble in this case was cut once only. Normally in control procedures cutting is more frequent so that the bramble is not allowed to recover completely.

277. OBSERVED AND EXPECTED VALUES When the calculations of expected values for the different plot measures were made for the regrowth plots, there were a large number of uncertainties. It was assumed that the distribution of dry weight between components in the permanent plots in 1975 was the same as for the same period in 1974, in the harvest plots. Dry weight of stem components was assumed to be roughly correlated with length. On the whole agreement between observed and expected values was reasonable.

TABLE 50 WYTHAM REGROWTH COMPARED WITH REGROWTH
AFTER 2.4.5 T. SPRAYING (AMOR 1971)

Table 50

	Leaf cover	Primocane growth
Amor (1971)		
<u>R.prccerus</u>	43 % controls	24 % controls
<u>R.ulmifolius</u>	81 ..	96 ..
Wytham 1st yr. regrowth		
1974	36 ..	68 ..
1975	38 ..	58 ..

278. REGROWTH AFTER 2, 4, 5, T. SPRAYING Amor (1971) measured regrowth of plots of R. ulmifolius and R. procerus after they had been sprayed with 2.4.5.T. in the spring. There was no regrowth until the autumn following spraying and the dry weight of the plots was then measured the following summer i.e. after 15 months. The strong regrowth shown by the plots in Wytham was also shown in Amor's results(^{P.168} ~~Table~~ 50).

279. SHOOT REMOVAL AND REGROWTH ENVIRONMENT The clearing away of the bramble shoot system alters the local environment in which regrowth occurs. Root competition was probably not greatly altered, but above ground, competition for light was reduced in the first year. Any increase in photosynthesis and growth that this allowed, was insufficient to compensate for the effect clearing appears to have had on rootstock reserves. Humidity, soil temperature and other factors were also altered which could affect bramble regrowth in unpredictable ways.

280. TOP-GROWTH REMOVAL AND ROOT RESERVES The reduction in the regrowth following removal of the top growth in autumn is thought to have been caused by a diminution of root reserves. During autumn, die-back of second year canes occurs and some of the material from these may be returned to the rootstock. During autumn, also, photosynthesis occurs in first-year canes. Some of the products of this form the cane reserves on which lateral growth is based. Others may be returned to the roots to replace the material used to support first-year cane growth. Early autumn clearing of the top growth would prevent these types of return and so weaken the plant.

281. INVASION OF CLEARED AREAS BY OTHER SPECIES Amor (1971) found that non-bramble species increased following killing of bramble top growth.

In Wytham there was no sign of an invasion either by non-bramble species or by bramble seedlings following clearance of top growth. The soil surface in the Wytham clearings was not very favourable for establishment because of the trampling that had occurred. The site was shaded whereas Amor's was in the open. Neither the trees above, which were too young, nor the surrounding bramble bore much fruit so that there was no immediate, large source of propagules to invade the cleared area. Regrowth of bramble in Wytham started in the spring following autumn clearing. There was thus little time for other species to establish before bramble competition was resumed.

TREE COMPETITION AND BRAMBLE GROWTH

INTRODUCTION

282. The large variations in bramble growth that occur within woodlands depend partly on the intensity of tree competition, particularly the nature of the tree canopy. This was shown quantitatively in the differences in bramble occurrence between stands of different tree species. (Ovington 1955). It is well known that growth of bramble increases under gaps in the tree canopy and for beech, Watt (1925) measured variations in growth under gaps of different sizes.

283. WYTHAM MEASUREMENTS The patchiness of growth in Area C was related to variations in tree canopy composition. The results from two surveys of the vegetation in Wytham were used to examine this effect over larger areas of the wood.

284. The differences in growth were measured between bramble under breaks in the tree canopy and under the surrounding shade. Six small gaps were created by the removal of a few trees. The changes in bramble growth that resulted showed the response of the plant to a change in tree competition, the rate at which growth changed, and the establishment of large differences in growth between adjacent stretches of bramble.

PATCHINESS IN AREA C

285. The tree species above each of the harvested plots in this area were noted. Oak covered about half the plots while five other species contributed from 4 - 20% total cover. ^{P. 174} Table 51 gives mean bramble

dry-weight per plot over^{all} the harvests for the different tree species. The patchiness in growth largely corresponded with differences in the distribution of the tree species.

286. CONFOUNDING OF HARVEST AND TREE SPECIES EFFECTS Dry weight per plot of bramble varied with the harvest. As the different tree species were not equally represented at each harvest some confounding of harvest and tree species effects occurred. Plot dry weights were converted to a relative scale to overcome this and then means for the different tree species calculated. This had little effect however on the relative differences between tree species shown in the first column of Table 51. ^{P.174}

287. OTHER CAUSES OF VARIATION The total area of the stand, containing these plots, was small. There were no obvious changes of soil, slope or aspect within it. All the plots were more than 15 metres from the nearest ride. Over the three years of observation there was little change in the bramble growth over the area which indicated that the population was relatively stable. It seems unlikely therefore that differences other than variations in tree competition were responsible for the differences in growth observed.

288. LENGTH GROWTH OF CANES UNDER OAK AND SYCAMORE In 1975 the growth of two groups of seven, first-year canes were compared. One group was under oak, the other under sycamore, about 4m away. The differences in growth of individual canes reflect the differences in dry weight per unit area under these two tree species(^{P.173} Figure 58),

289. DISCUSSION Beech and sycamore had the greatest effect in suppressing bramble growth in C, oak the least, while larch was

FIG. 58

BRAMBLE GROWTH UNDER DIFFERENT TREE SPECIES

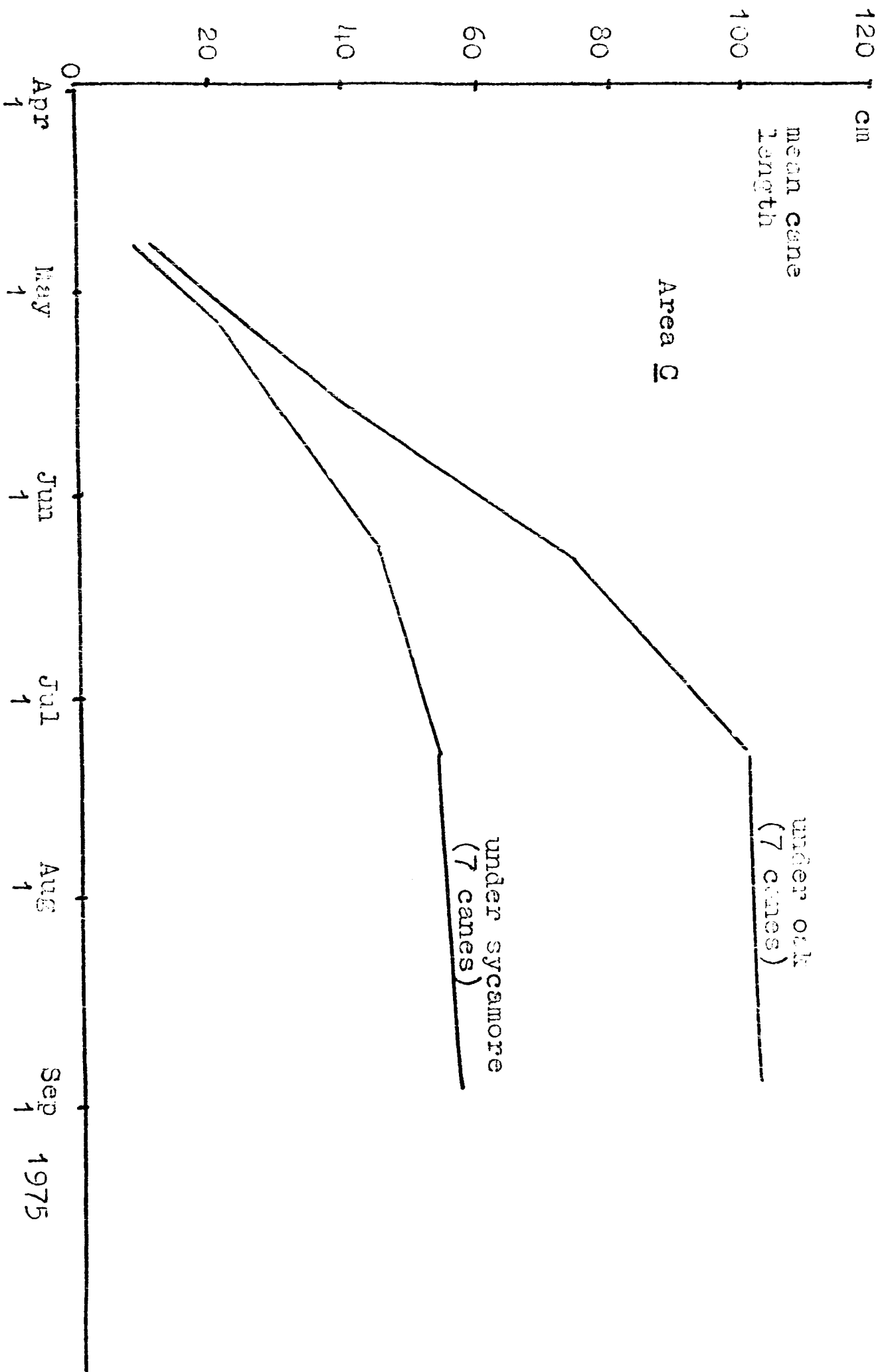


TABLE 51

BRAMBLE DRY WEIGHT UNDER DIFFERENT
TREE SPECIES IN AREA C

Table 51

Tree species	No of plots under each species	Mean plot dry weight g/sq.m	Mean relative-dry-weights (a)	(b)
Oak	46	167.8 ±10	1.32	1.00
Ash	5	132.4 ±25	1.12	0.86
Larch	12	113.2 ±25	0.89	0.70
Hornbeam	4	111.5 ±33	0.92	0.63
Beech	13	78.3 ±13	0.62	0.31
Sycamore	20	67.6 ±14	0.56	0.42

Mean relative-dry-weights for each tree species were calculated as follows:-

(a) Mean value for all harvests of

Bramble dry weight per plot under that
tree species at a given harvest

Mean bramble dry weight per plot under
all tree species for that harvest

(b) was derived in a similar way but mean dry weight per plot under oak only was used as the denominator instead of mean dry weight for all species.

TABLE 52

% COVER BY BRAMBLE IN WYTHAM
AS MEASURED BY ECOSIG SCORE

Table 52

Ecosig score	%of plot covered by bramble	No of plots in each score class	Total area covered by bramble
0	0	21	0 plot-equivalents
1	0-5	24	0.6 "
2	5-25	31	4.6 "
3	25-50	35	13.1 "
4	50-75	26	16.2 "
5	75-100	26	22.8 "
		163	57.3 = 35% total area

Plot-equivalents are obtained by assuming that the mean %cover for each score class is equal to the mid-point of the class interval

intermediate. Because ash and hornbeam were only poorly represented their positions relative to oak and sycamore may not be typical. The growth of bramble under pure ash in area A, for example, was much greater than under the pure oak canopy of area B. The ash trees in C, however, were small, isolated trees in an overall canopy of much denser foliage. In general, canopy density appeared to be playing a major role in the variations in the bramble growth beneath different tree species.

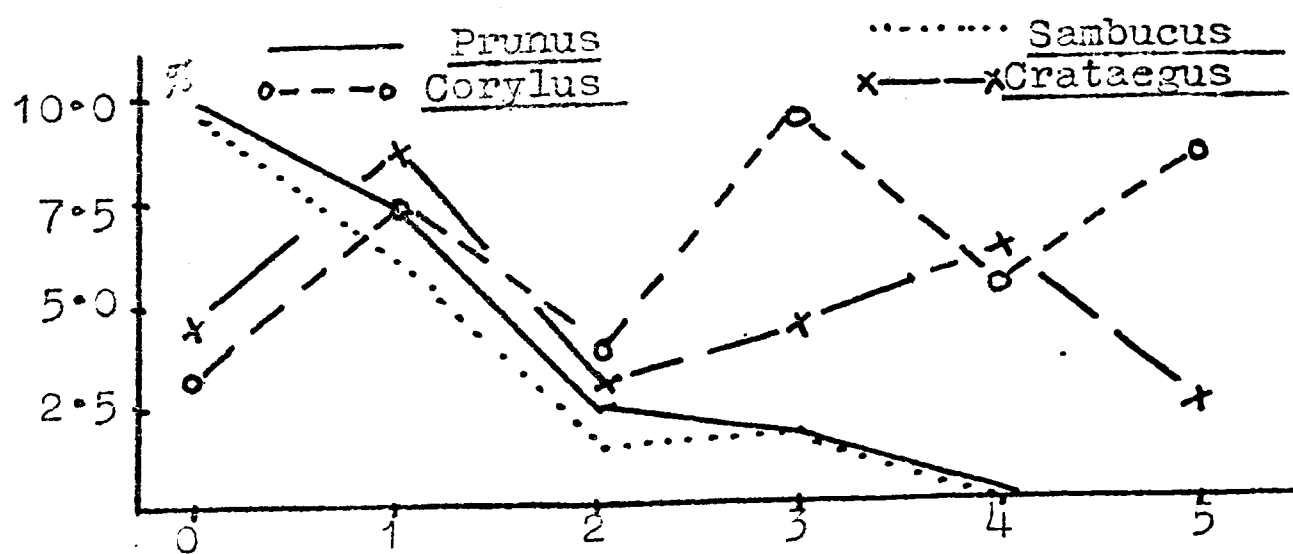
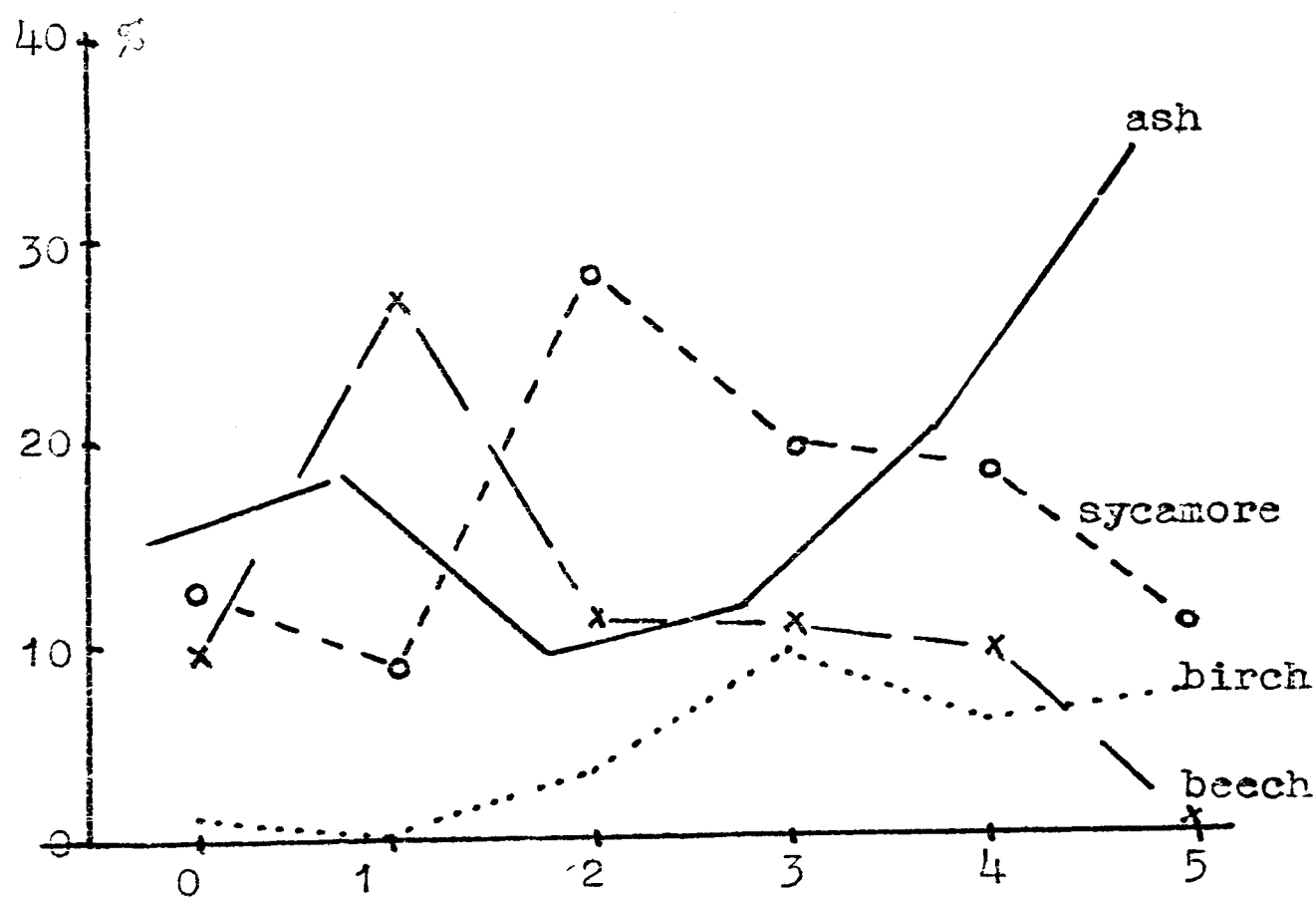
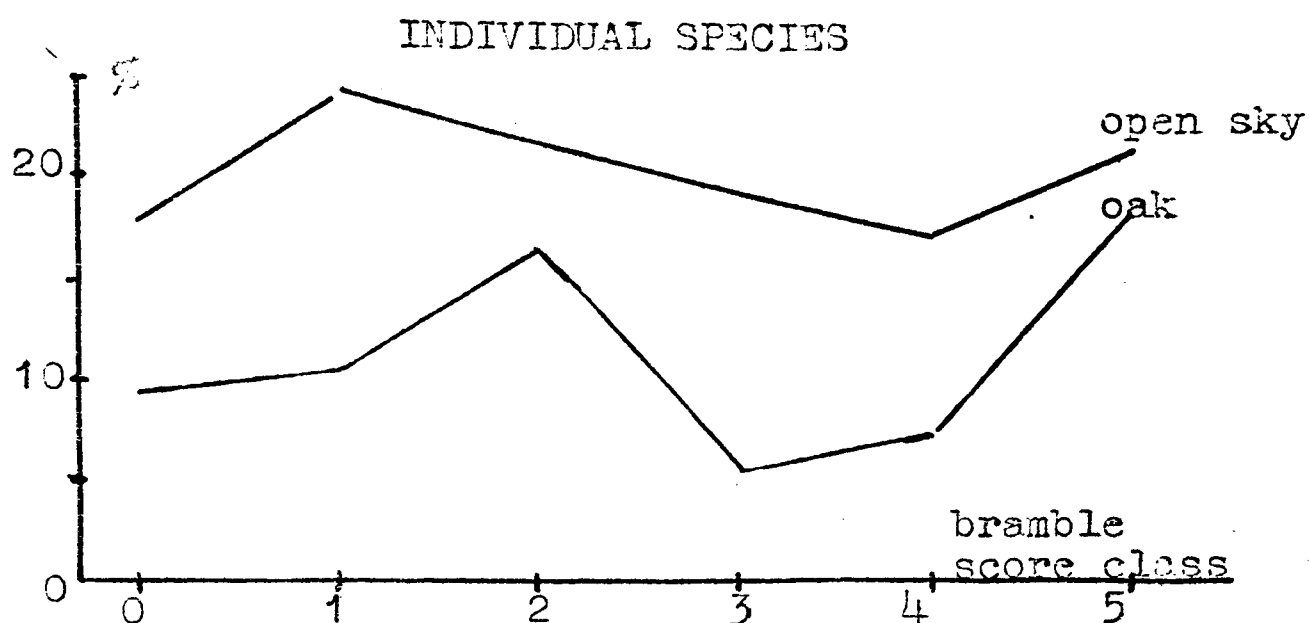
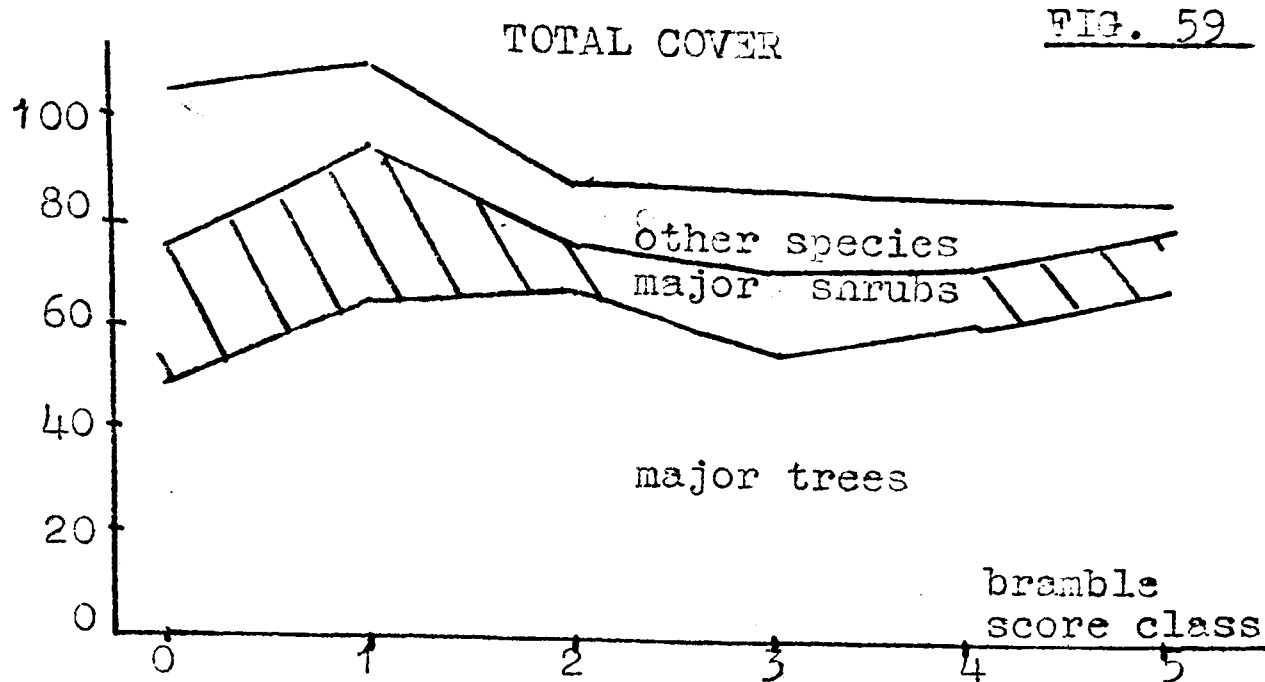
THE WYTHAM SURVEY

290. In 1974 Field and Dawkins (in prepn.) collected data on the vegetation from all over Wytham Woods. From these results I extracted the following material and used it to compare tree canopy variations and bramble growth.

291. THE RECORDING UNIT The sampling unit was a square plot, ten metres by ten metres. Within this were made observations of tree cover, density etc. as well as observations on the composition of the undergrowth. The measurements of most use to me were bramble "ecosig" score and the tree canopy composition.

292. "ECOSIG" SCORE The "ecosig" score was a 0-5 scale based on the percentage cover of bramble in the plot(^{P.174} Table 52). If it is assumed that the mean bramble cover for the plots in each of the "ecosig" score classes equalled the half-way point in that range, the approximate area totally covered by bramble in Wytham can be obtained. This was equivalent to about 35% of the wood. Bramble was present in 87% of the plots.

293. TREE CANOPY COMPOSITION The percentage cover above the plot at 2.5m height and greater was split into the different species that



OVERSTORY COMPOSITION FOR WITHAM SURVEY PLOTS
RELATIVE TO BRAMBLE GROWTH

contributed to it. Each species was assessed separately and the percentage of open sky was also noted. Total cover over the plot in the height range 0.5 - 2.5m was also recorded but not split according to species. Bramble itself contributed to this cover, so it was not possible to deduce the shrub cover above the bramble. The contribution of the different tree species to total canopy cover (above 2.5m high) was determined for each "ecosig" class.

294. TOTAL CANOPY COVER ABOVE BRAMBLE The bulk of the plots were within woodland. Only a few were on open areas, rides etc., within the wood boundaries. Total cover over the different "ecosig" classes was thus high and fairly consistent. Open sky was also fairly constant at about 20% cover for all six "ecosig" classes (Figure 59), ^{P.176}

295. MAIN TREE SPECIES Five tree species made up 65% of the total canopy cover. Over the six classes there was a change in the relative abundances of these. Birch and ash increased their contribution over the denser bramble stands while that of beech and sycamore decreased. Oak varied from 5-18% total cover for the different "ecosig" classes, but showed no overall trend.

296. The "O" "ecosig" score presented some difficulty of interpretation as many of the plots in this class were rather unusual e.g. on rides, where periodic mowing prevented bramble establishment. The absence of bramble was thus not always a result of its inability to grow under that level of tree competition.

297. The results for sycamore and beech fit with those from Area C that high cover of these species is associated with a low level of bramble growth. The ash pattern fits with the vigorous bramble growth found in

area A. There is thus a marked contrast between those species which cast a fairly dense shade, such as beech or sycamore, and trees which cast a light shade such as ash and birch. The lack of a trend for oak is surprising considering the relatively high growth found under this species in area C. A possible reason for this is considered on page 196.

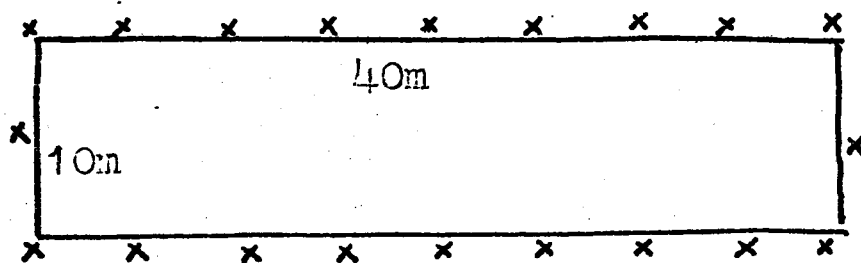
298. **SHRUBS** The four main shrub species - 19% total cover - showed two patterns with respect to the bramble growth beneath them. Prunus spinosa and Sambucus nigra decreased as the "ecosig" score increased, while Crataegus sp. and Corylus avellana remained fairly constant. The latter two species occur more frequently than the former pair as undershrubs in Wytham. Conditions which favour bramble growth may also favour growth of undershrubs. This positive association may offset the depressing effect a shrub layer normally has on the bramble below.

299. **OTHER SPECIES** The other tree and shrub species which contributed to the canopy above 2.5m occurred too infrequently for any conclusions to be drawn about their relations with the bramble layer. Many were found only in one or two plots.

300. **PROBLEMS IN THE USE OF THE SURVEY DATA** Where more than one species was present in the canopy (including open sky as a species) it was not possible to tell which species was directly over any bramble growth. There was no information on the overlapping of species in relation to the bramble layer. With this size of plot (10 x 10m) considerable differences in bramble growth could exist between one part and another within the same plot. There was also no way of determining the extent of any shrub layer less than 2.5m high.

PLAN OF Dr P.S.LLOYD's SAMPLING UNIT

x = a metre-square plot . These were used to examine the relation between bramble growth and overstorey.



There were 32 sites.

VEGETATION SURVEY CARRIED OUT BY DR. P.S. LLOYD

301. Some of the problems inherent in the survey of Field and Dawkins were not encountered in the analysis of results obtained by Dr. P.S. Lloyd. His sampling units, ^{P.179} (Figure 60) were sited in stands mainly in the northern part of the wood. For my purposes, the data from the twenty, metre-square plots, round the outside of the sampling unit, was used.

302. DATA RECORDED For each metre-square plot figures were available for bramble cover on a 0 - 5 scale ^{P.181} (Table 53) shrub cover on the same scale and the tree species forming the overstorey. Bramble height and shrub height, though recorded, did not prove useful in the following analysis.

303. Because the plots were smaller than those used by Field and Dawkins a higher proportion had a single species overstorey. Bramble was present at all the thirty-two sites, thus absence of bramble from a plot was less likely to be a result of propagules failing to reach the plot, rather than inability to grow in the plot.

304. The plots were treated as being independent samples, although, in fact, grouped in blocks of twenty. The plots were five metres apart, and over this distance considerable changes in both overstorey and bramble growth can occur. Thus the treatment of each plot as independent was felt to be justified.

305. OVERSTOREY SPECIES Only three species contributed significantly to the overstorey in the parts of the wood covered by this survey - oak, ash and sycamore. Their relation to the growth of bramble beneath them is

TABLE 53

% COVER SCALE USED FOR
METRE-SQUARE PLOTS

Table 53

% cover (bramble or shrub)	Scale value
0	0
0-20	1
20-40	2
40-60	3
60-80	4
80-100	5

TABLE 54

NEGATIVE ASSOCIATION BETWEEN
BRAMBLE-COVER SCORE AND SHRUB-COVER FOR
INDIVIDUAL SPECIES

Table 54

	r^2
<u>Corylus</u>	0.20
<u>Crataegus</u>	0.52
<u>Sambucus</u>	0.38

r^2 was not calculated for Prunus because 14 out of 18 plots had a Prunus score of 5, bramble score 0 .

TABLE 55

OCCURRENCE OF DIFFERENT SHRUB SPECIES
UNDER ASH & SYCAMORE OVERSTOREY

Table 55

	Ash	Sycamore
	No of plots	
Shrub layer species		
<u>Prunus</u>	18	1
<u>Corylus</u>	14	3
<u>Crataegus</u>	17	9
<u>Sambucus</u>	8	37
Sycamore saplings	1	16
Ash	0	45
Other species	26	16

FIG. 61

numbers
of plots
180

170

60

50

40

30

20

10

0

under sycamore

FREQUENCY OF ASH, OAK, &
SYCAMORE OVERSTORIES FOR DIFFERENT
DEGREES OF BRAMBLE COVER

(a)

all plots for each
species

under ash

under
oak

bramble cover class

numbers
of plots

40

30

20

10

under
oak

under sycamore

(b)

only plots with no
shrub cover

under ash

Mean %
bramble cover
per plot
Ash = 61
Oak = 50
Sycam. = 16

0

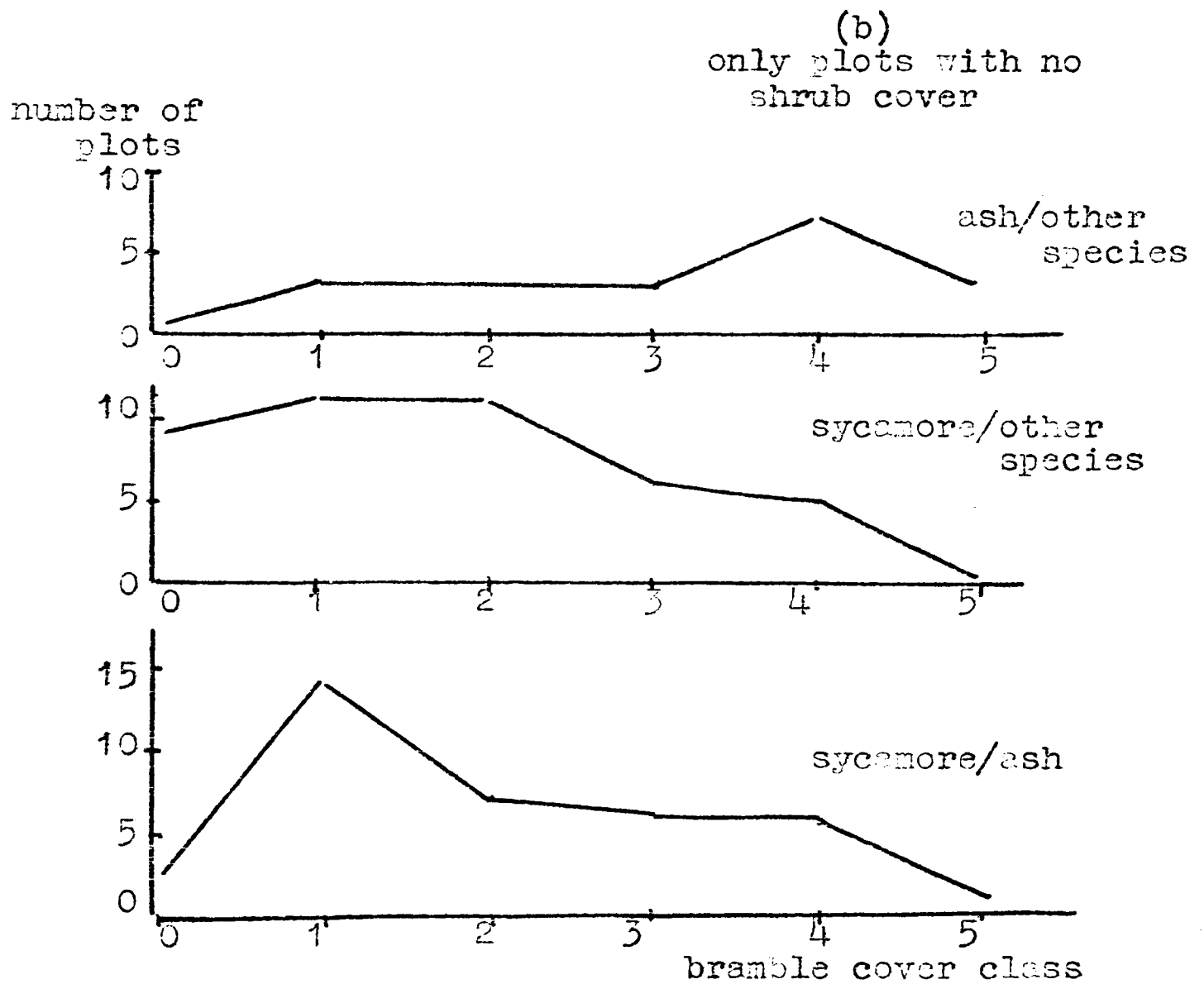
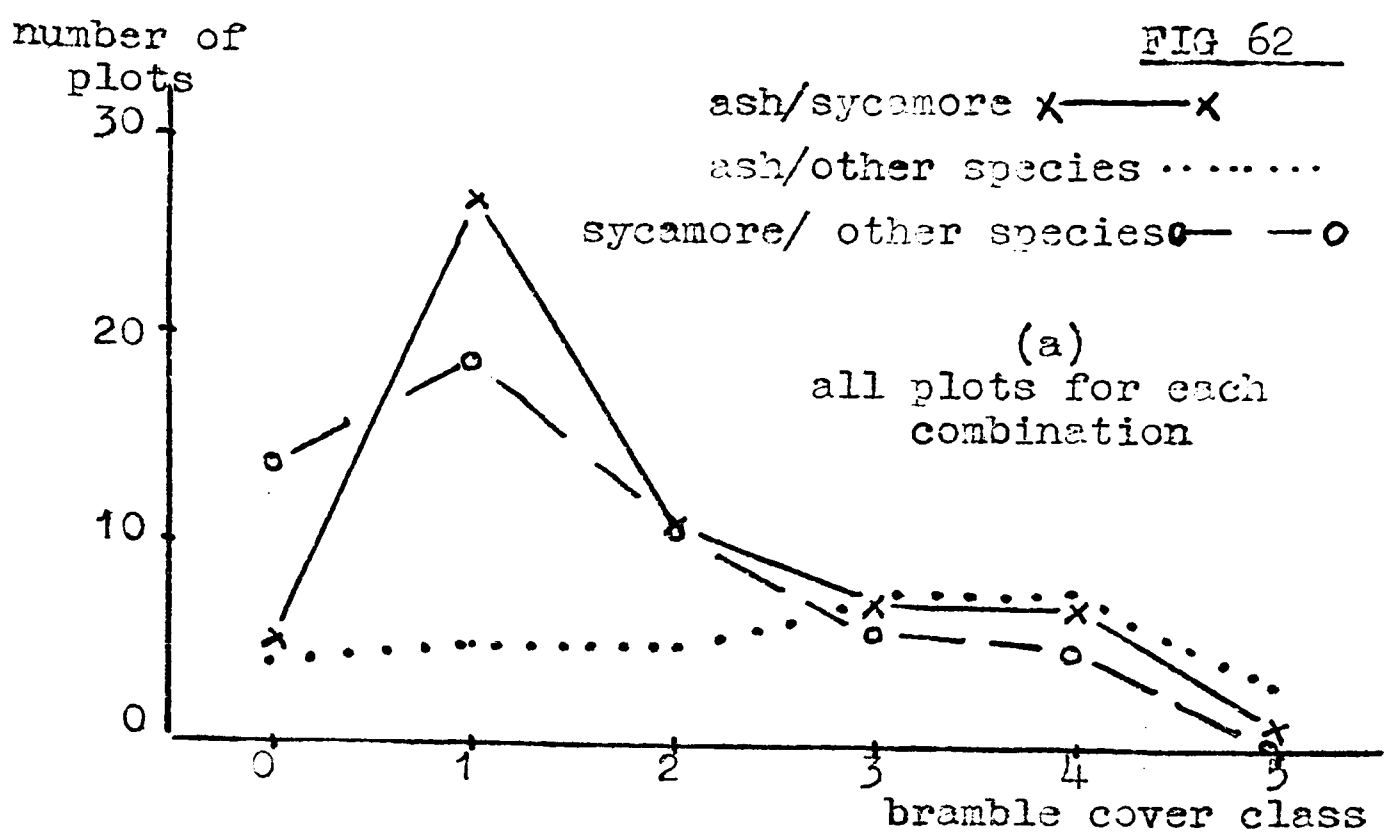
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2

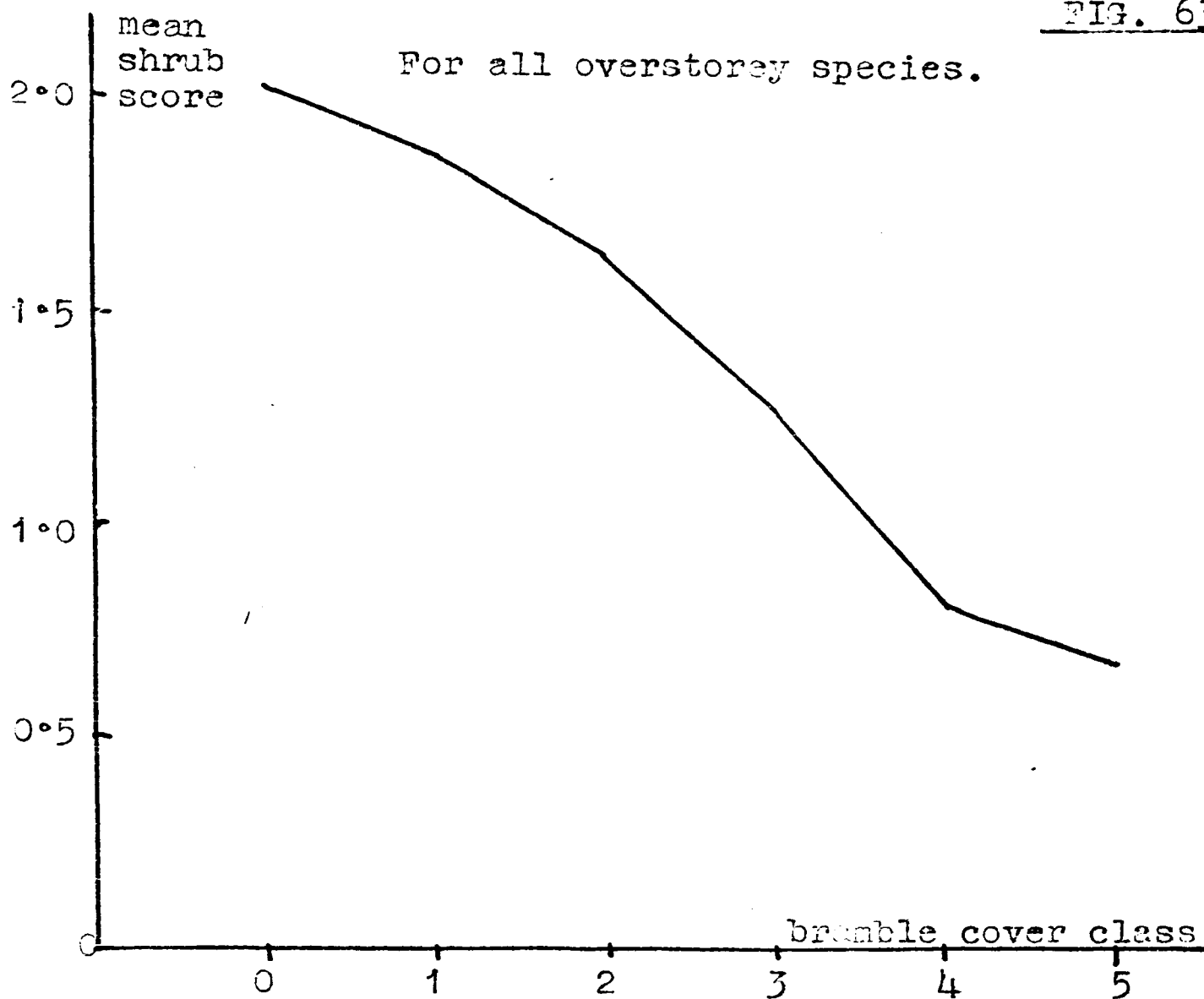
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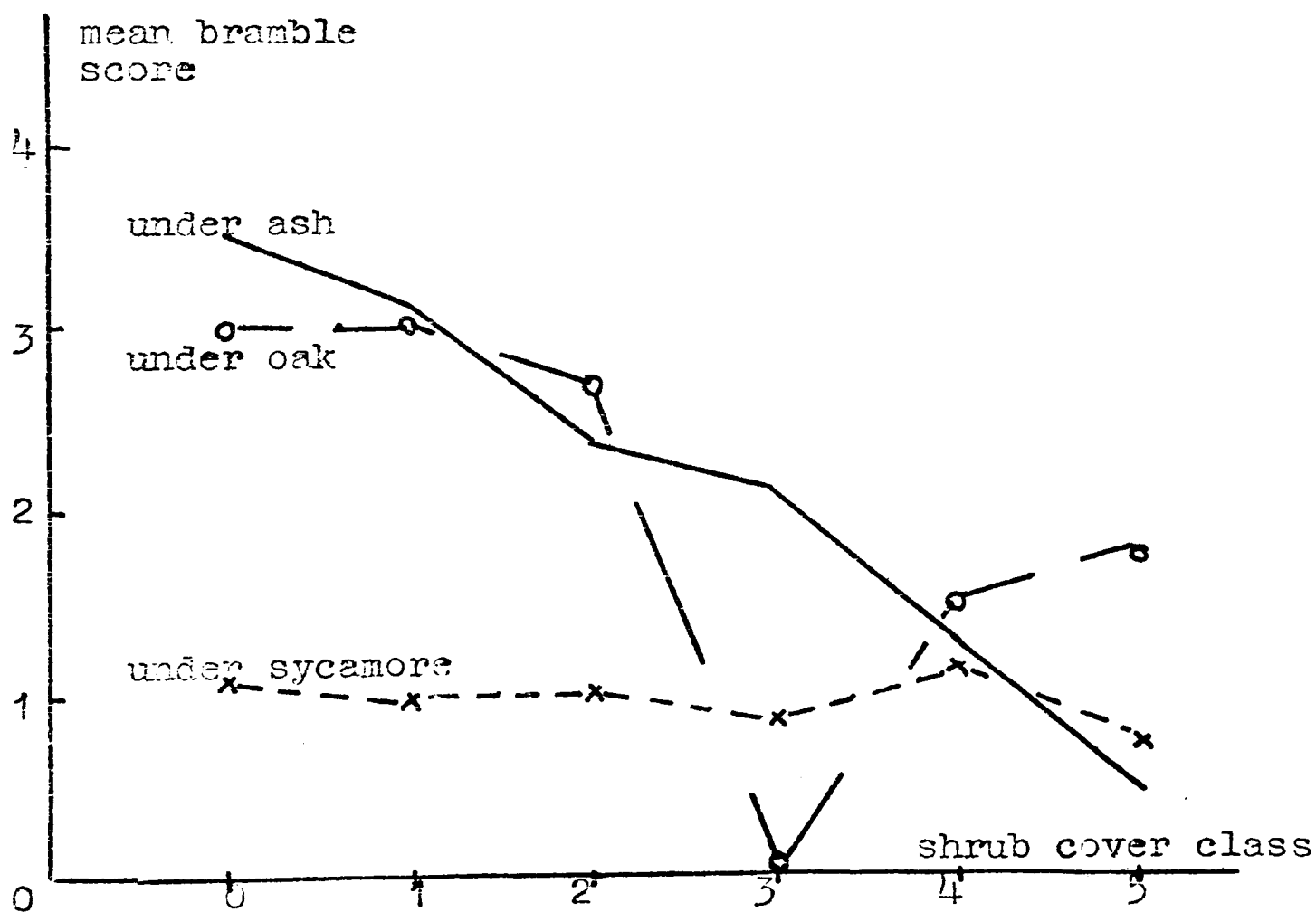


PLOTS WITH TWO SPECIES IN THE OVERSTOREY



MEAN SHRUB SCORE ABOVE DIFFERENT DEGREES OF BRAMBLE COVER

FIG. 64



BRAMBLE COVER UNDER DIFFERENT OVERSTOREIES WITH INCREASING SHRUB COVER

^{P.182}
 shown in Figure 61. The influence of a shrub layer in modifying the effect of the overstorey species was clear. Where two species were present, in the overstorey, the effect on the bramble was intermediate between the two "pure" canopies (^{P.183} Figure 62).

306. The tree canopies tended to be at the same height, hence the presence of one species prevented the other from occupying the whole of the canopy above that plot. One species thus tended to "dilute" the effect of the other e.g. ash in sycamore. This contrasted with the tree: shrub relation, where, because their canopies tended to be at different heights, both could expand over the whole plot and the effects on the bramble were additive.

^{P.184}
 307. EFFECT OF SHRUB LAYER Figure 63 shows the decline in mean shrub score above increasing bramble cover for all the plots. The effect of the shrub layer was modified by the nature of the overstorey. Whereas under an ash canopy the amount of bramble cover was related to the shrub cover, the sycamore overstorey tended to override any additional shrub effect. Oak showed a less pronounced decline than ash in bramble growth with increasing shrub cover. The lower number of oak plots in total increased variability, there being only one oak plot with a shrub score of 3.

^{P.181}
 308. INDIVIDUAL SHRUB SPECIES Table 54 gives r^2 (coefficient of determination) of bramble score vs shrub score for individual species under an ash canopy. The lowest r^2 was for Corylus which in the Wytham Survey (^{P.176} Figure 59) showed no downward trend with increasing bramble cover. Crataegus, which also showed only a weak downward trend in Figure 59, here had the highest r^2 .

309. The species found in the shrub layer differed for the two main

overstorey species(^{P.181} Table 55) Watt (1924) found that beech regeneration was suppressed by vigorous bramble growth. The greater sapling growth under sycamore, where the bramble cover was low, may be a similar situation. Under ash, the mean bramble score only becomes as low as under sycamore with the highest shrub cover score. In this class the high shrub cover may replace the bramble layer in suppressing sapling growth.

The factors which might lead to differing growth of bramble under different tree species are considered after the description of the response of bramble to gaps in the tree canopy.

GROWTH OF BRAMBLE UNDER "OLD" GAPS

310. Measurements of bramble were made under two "old" gaps, to determine the difference between growth directly below them, and below the surrounding canopy. One gap was in area D and about 7m across. Its age was not known. The other was in Bagley Wood (south west of Oxford) in abandoned oak'coppice. The gap, about 18m across, was created in 1968-69 by the poisoning of the trees in it. Thus at the time of the measurements it was 5-6 years old.

311. AREA D GAP Two transects were laid out, N-S, E-W, which crossed in the centre of the gap. Metre-square plots were recorded at 3m intervals along the transects on October 18, 1974. ^{P.188} Figure 65 shows the changes in A.I.V., I.V., leaf hits, along the transect. ^{P.187} Table 56 compares mean values for the five plots below the gap with the eight in the surrounding shade. ^{P.189} Figure 66 shows canopy profiles.

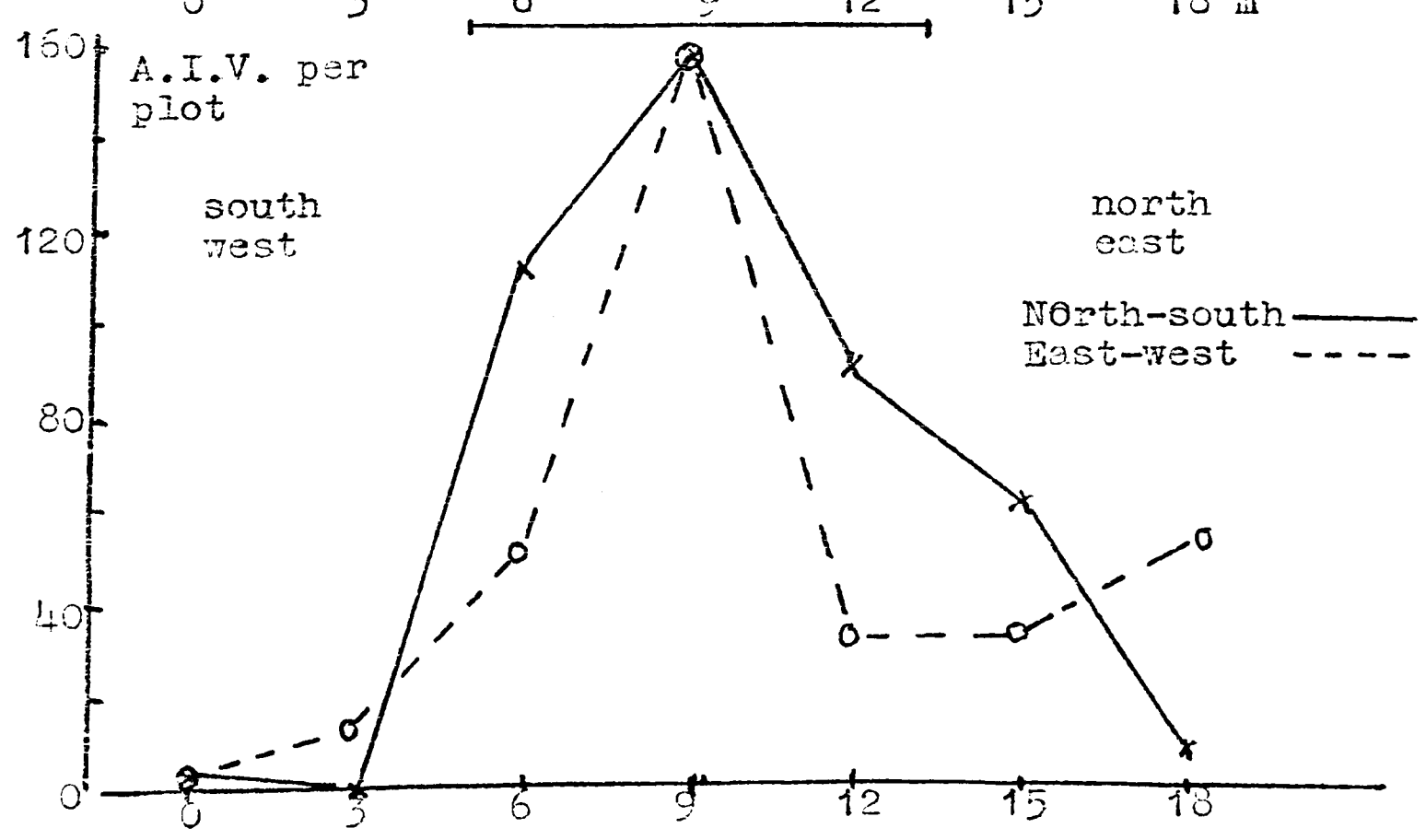
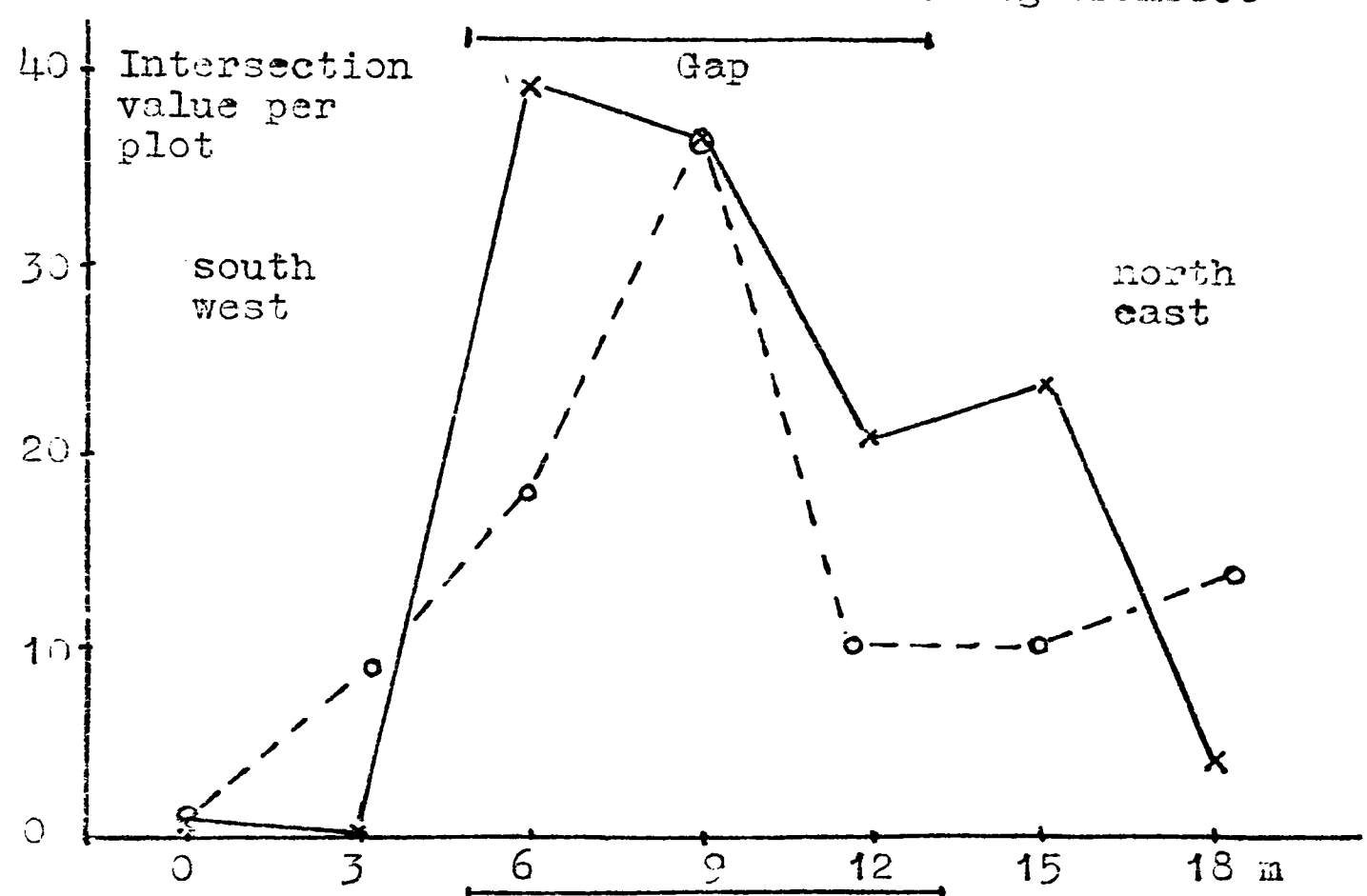
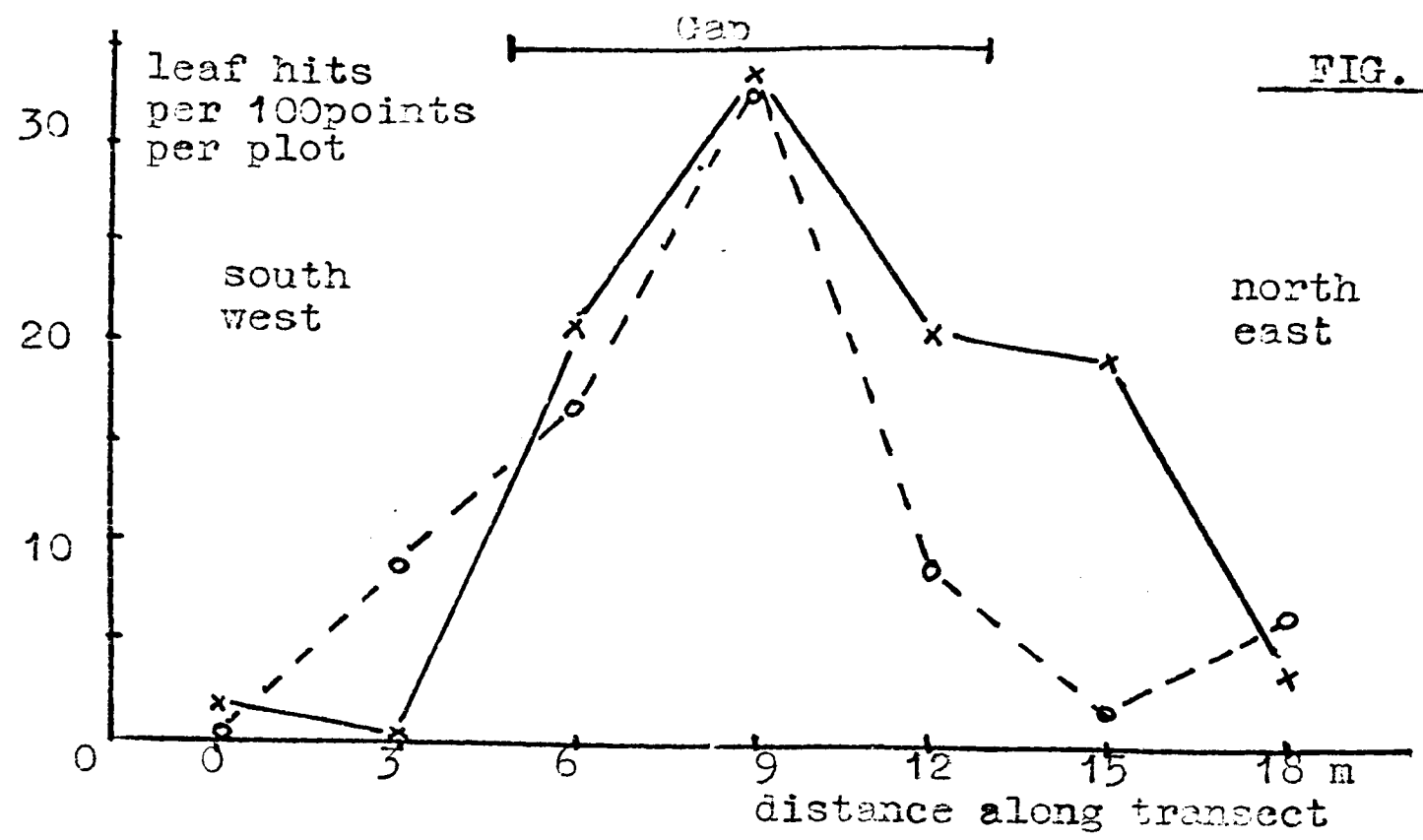
312. There was a sharp increase in bramble growth immediately below the gap. The influence of the gap spread outwards more to the north and east than to the south and west. As the stand faces west, the former are

TABLE 56

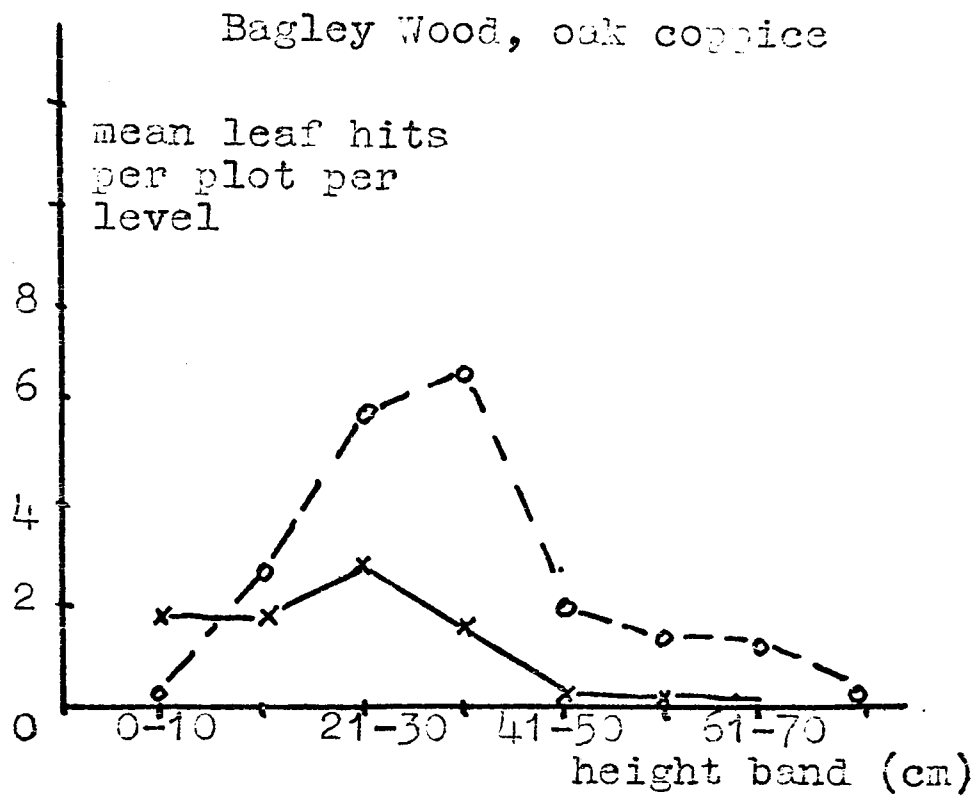
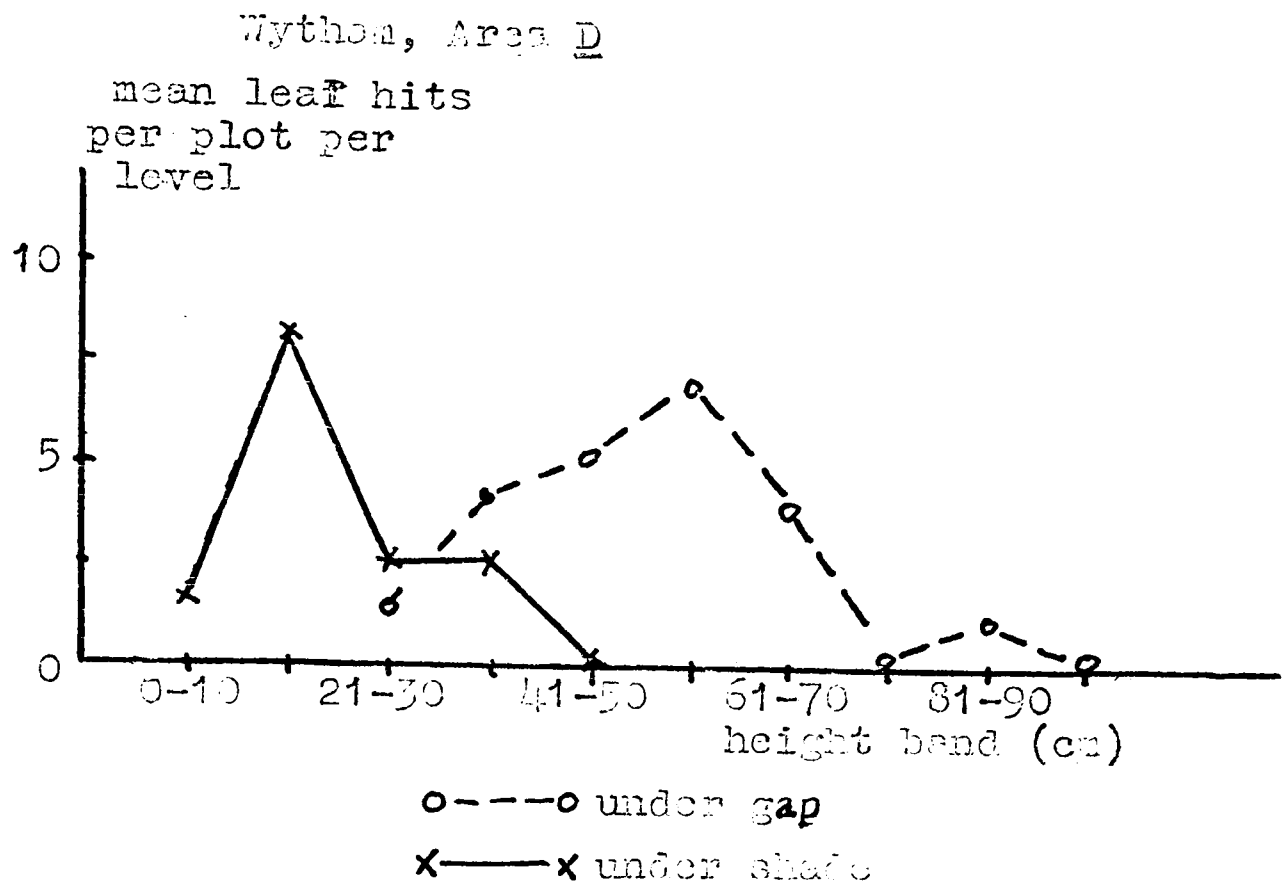
INCREASE IN BRAMBLE GROWTH UNDER GAPS
IN THE TREE CANOPY

Table 56

	<u>Under shade</u>	<u>Under gap</u>	
Area D	8 plots	5 plots	
mean values			
Leaf hits	5.5 ±2.4	20.4 ±4.0	per/sq.m
I.V.	7.7 ±2.8	25.0 ±5.6	"
A.I.V.	21.1 ±8.9	88.2 ±22	"
Bagley Wood site	5 plots	4 plots	
mean values			
Leaf hits	15.8 ±4.2	25.8 ±3.4	"
I.V.	39.2 ±8.8	76.5 ±11.9	"
A.I.V.	73.0 ±23	396.0 ±97	"
Estimated dry wt. from A.I.V.	86.9	209.7	"



CHANGES IN BRAMBLE GROWTH BELOW A GAP IN A BEECH OVERSTOREY



CANOPY PROFILES FOR BRAMBLE GROWTH UNDER
"OLD" GAPS

the directions receiving most side light from the gap.

313. **BAGLEY WOOD GAP** Four metre-square plots were recorded in the centre of the clearing and five in the surrounding coppice area on October 25, 1974. ^{P.187} Table 56, ^{P.188} Figure 66, show the difference that had developed in five years. There was also a considerable growth of grasses, tree seedlings etc. in the gap not found under the coppice.

314. These two areas showed that large differences in bramble growth developed within a few years of a gap being formed. The differences were largely confined to the area immediately below the gap, and could be detected using the standard methods of recording plots.

GROWTH UNDER GAPS CREATED IN WYTEAM

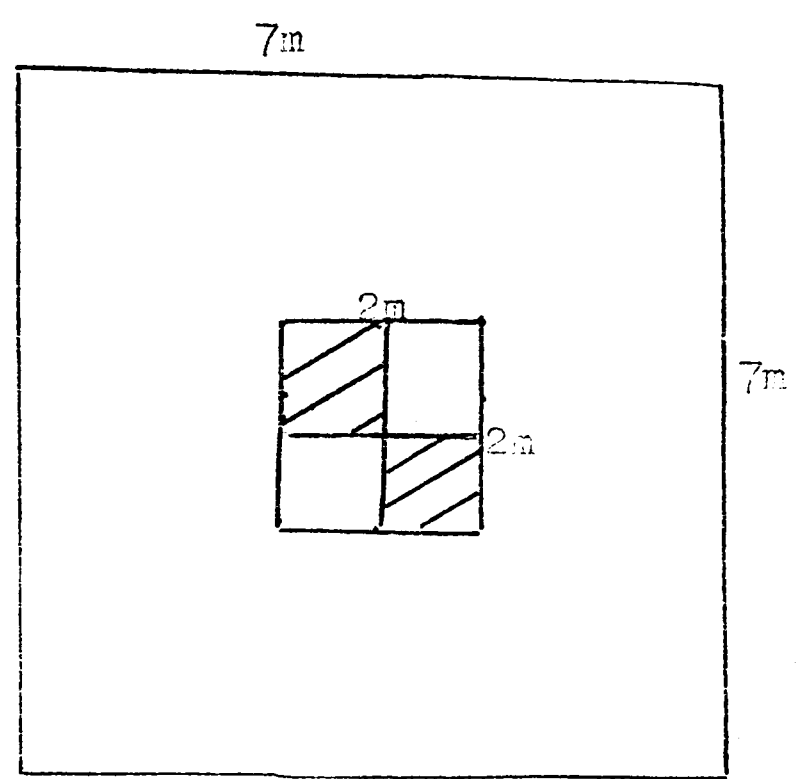
315. In January 1975 gaps were made in the tree canopy at three sites in Wytham, areas B, E, F (^{P.191} Figure 67) Two gaps were created at each site with two adjacent control areas of the same size. The central squares, in which were the plots to be recorded, were set out before any trees were removed. The trees in the gap were then cut down with as little disturbance as possible to the bramble below, particularly the central 2m square. The trees ranged from 5-7m in height and so were relatively easy to man handle.

316. **RECORDING OF PLOTS** The plots were recorded immediately before and after the trees were removed, and at intervals during 1975-76. The final recording was in July 1976. In the analysis the two plots in each 2m square were combined and the mean used. ^{P.192} Each point in Tables 57, 58 and ^{P.193-95} Figures 68-71 is thus based on six values.

317. **RESULTS** There was initially no significant difference between the plots in the clearings, where the trees were removed, and the controls.

PLAN OF THE CLEARINGS

In each area, B, E, F, there were four 7m x 7m squares.
The trees were removed from two, the other two acting
as controls.



= the metre-square plots
actually recorded

TABLE 57

COMPARISON OF PLOTS BEFORE AND AFTER
TREE REMOVAL FROM THE CLEARINGS

Table 57

	Before 28th Jan.	After 12th Feb.	
Leaf hits			
Clearings	43.6 ±5.1	46.0 ±5.1	per sq.m
Controls	36.2 ±6.1	35.3 ±6.0	"
I.V.			
Clearings	80.4 ±4.8	82.6 ±7.9	"
Controls	80.3 ±8.7	85.7 ±9.9	"
A.I.V.			
Clearings	359 ±32	351 ±41	"
Controls	388 ±59	407 ±54	"

TABLE 58

GROWTH OF BRAMBLE UNDER GAPS 1975-76

Table 58

	June 18th 1975	Aug.8th 1975	July 6th 1976	
Leaf hits				
Clearings	69.7 ±8.2	137 ±11.6	109 ±10.8	per sq.m
Controls	65.3 ±6.6	109 ±10.8	69 ±8.6	"
I.V.				
Clearings	114 ±9	129 ±6	152 ±7	"
Controls	104 ±10	115 ±8	123 ±8	"
A.I.V.				
Clearings	533 ±56	697 ±97	962 ±120	"
Controls	515 ±61	591 ±62	640 ±55	"

TABLE 58a

DRY WEIGHTS DERIVED FROM MEAN A.I.V.

	clearings	controls	
Feb . 1975	185	197	g/sq.m
" 1976	323	225	"
July "	426	281	"

CHANGE IN BRAMBLE CANOPY PROFILE

WITHIN A CLEARING

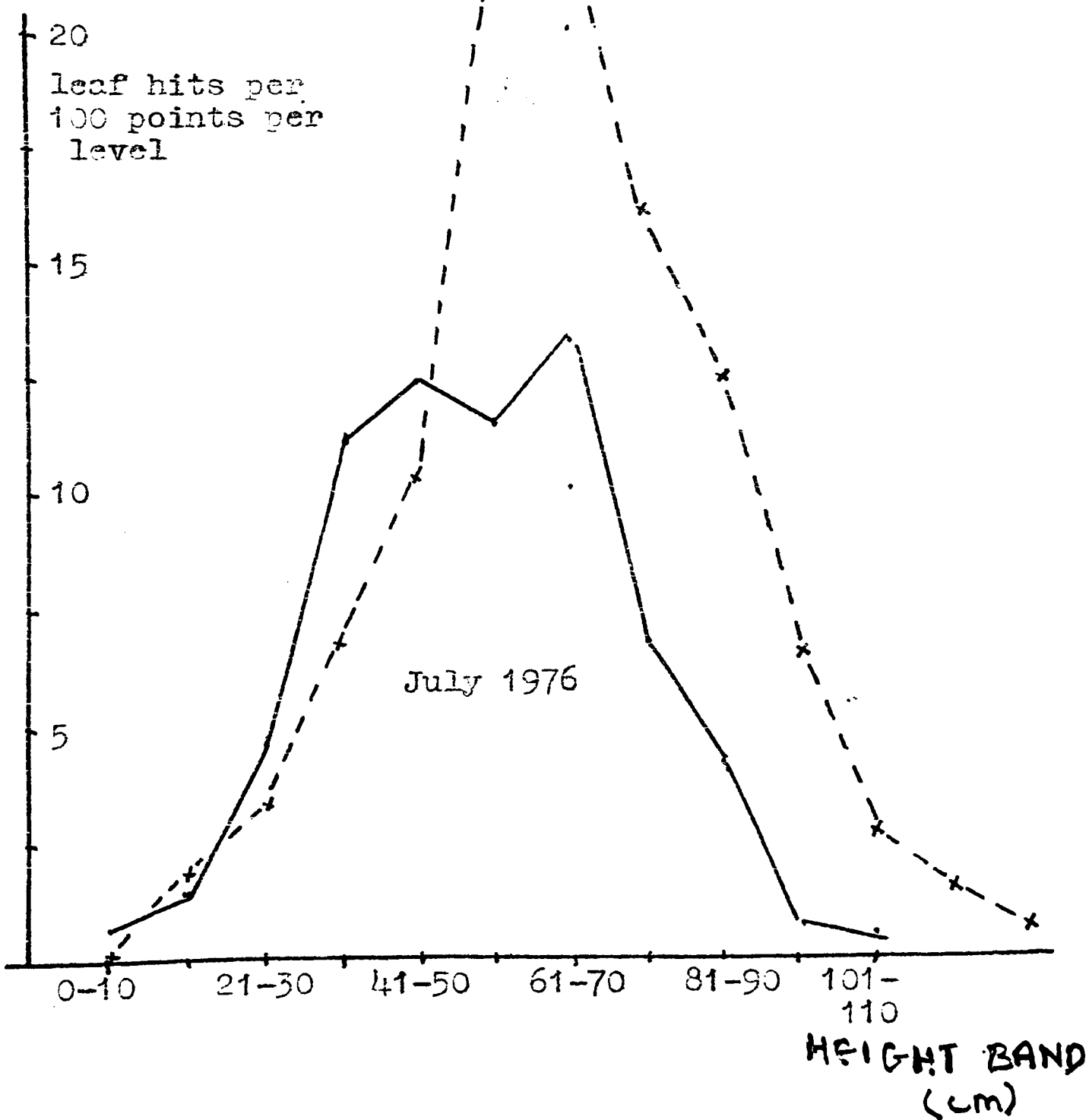
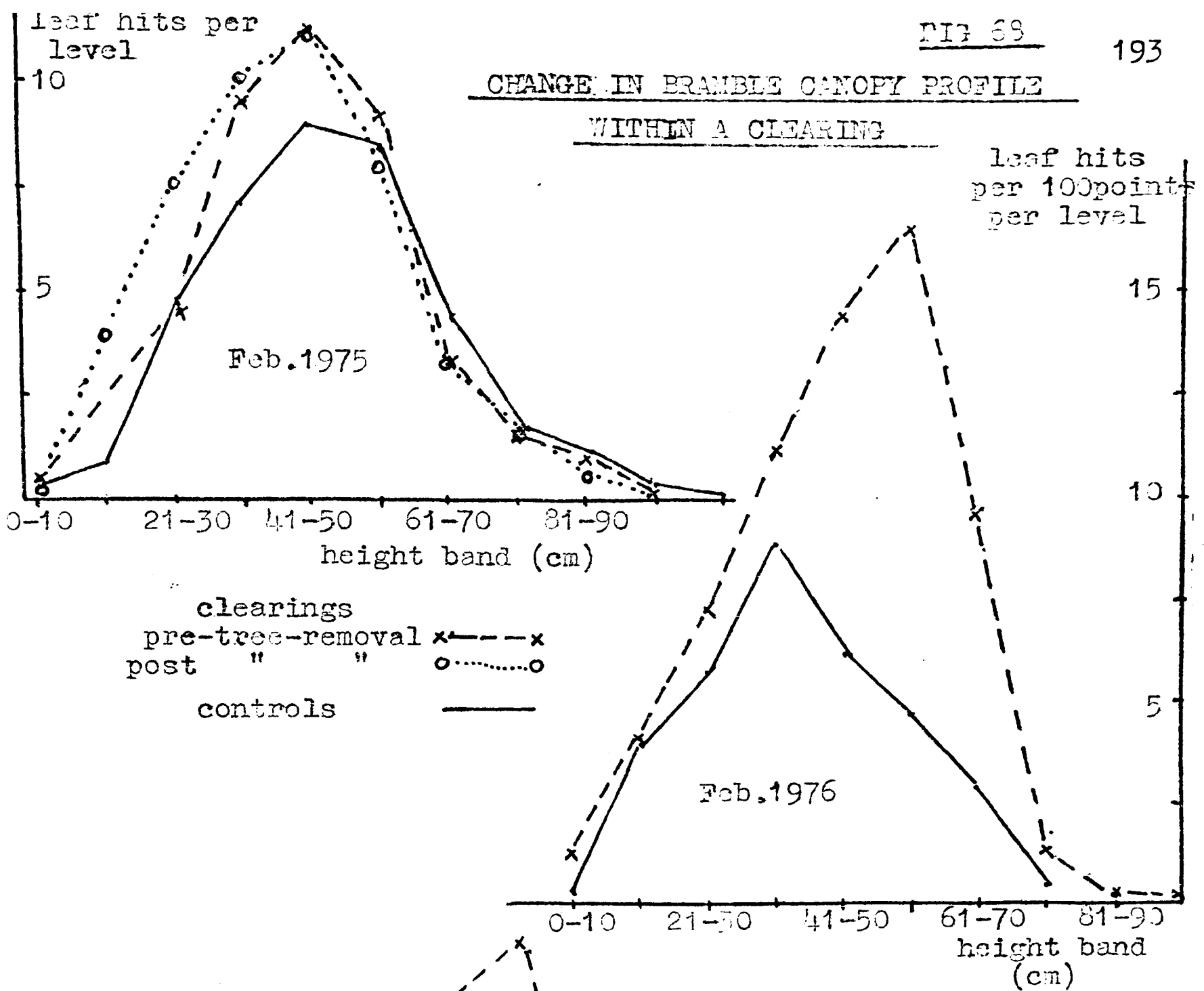


FIG. 70

CHANGES IN I.V. AND A.I.V. FOR BRAMBLE PLOTS FOLLOWING TREE REMOVAL.

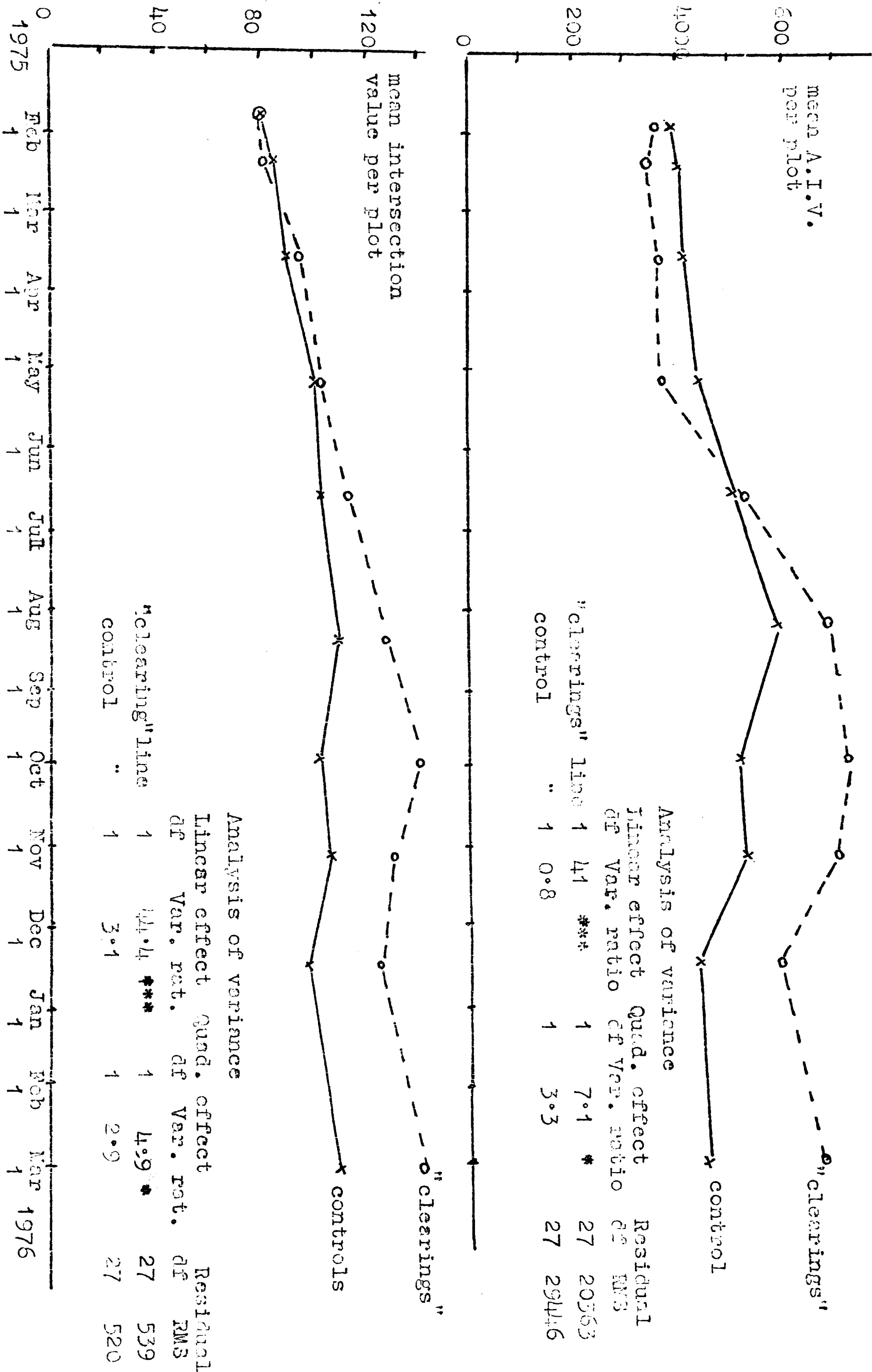
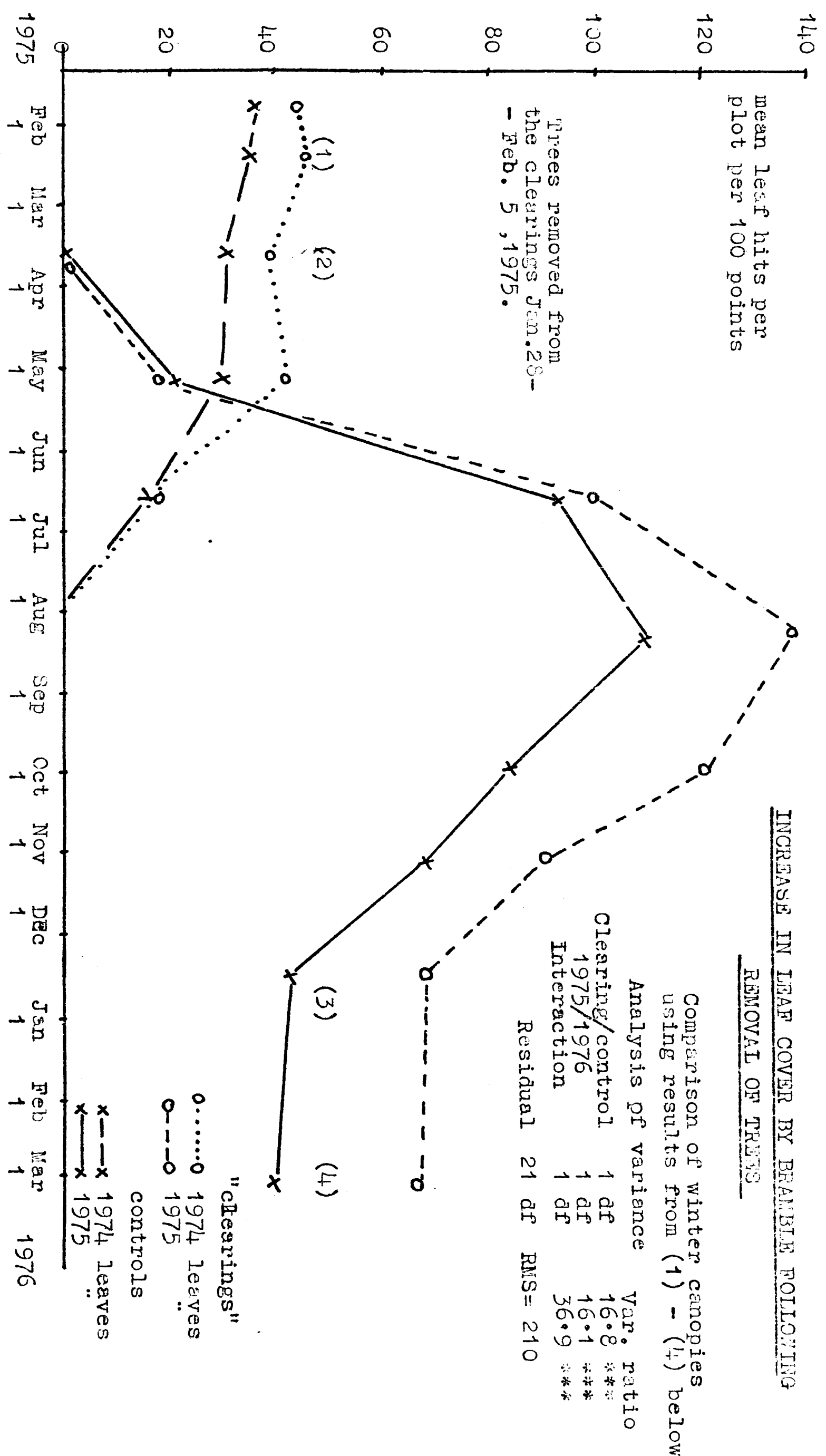


FIG. 71



The process of removing the trees did not affect the clearing plots,
 (Table 57, Figure 68) ^{P.192} ^{P.193} Differences between the two sets of plots started
 to appear in May when the tree canopies over the controls were expanding.
 Linear trends for I.V. and A.I.V. were significant for the clearing plots
 over 1975 ^{P.194} Figures 69, 70. The difference in leaf hits in winter 1975-76
 between the two treatments was significantly greater than the difference
 in winter 1974-75. The increase in growth continued in 1976 (^{P.192} Table 58),

DISCUSSION

318. TREE SPECIES AND CANOPY DENSITY The results from the first part
 of this chapter showed that much of the variation in vigour of growth was
 related to the species composition of the overstorey in different parts of
 the wood. The marked difference between ash and sycamore suggests that
 canopy density is important. This view is supported by the effect of a
 shrub layer being additive where the overstorey was light e.g. ash, but
 having little effect where the tree canopy was dense e.g. sycamore.

319. The nature of the tree canopy is affected by the age of the trees.
 The change in the bramble layer as tree stands age has been noted for beech
 by Watt (1924) and for pine by Ovington (1955). Oak was found in both
 surveys at a fairly constant level over the whole range of bramble growth,
 and was intermediate between ash and sycamore. This may be because of the
 difference between young closely-spaced oaks where the canopy is very dense
 and old, more widely spaced oaks with a rather sparse canopy. Both
 occurred in Wytham.

320. SPEED OF RESPONSE BY BRAMBLE In area C large differences in
 bramble growth occurred over distances of a few metres in response to tree
 species differences. Such localised variation was also found under gaps.
 Such changes were shown to develop very quickly following change in tree

competition. The speed of response may be partly governed by the amount of bramble already present. In the clearings created in Wytham the initial bramble level was about the middle of the range found in this wood. The rootstocks were well-established. In an area where growth was less vigorous to start with, the initial response to a gap in the canopy might be less.

321. MECHANISMS OF TREE COMPETITION No direct experiments were performed to determine the mechanisms by which tree and shrub competition affect bramble growth. The various observations point to canopy density being the important factor, probably acting through interception of light. Other possibilities are considered below.

322. The tree canopy alters the distribution and amounts of water reaching the ground. Anderson (1959) found that increased growth of herbs, relative to under the shade, was correlated with the size of canopy gap above them. The correlation with increased water availability, however, was greater than that with increased illumination in the gap.

323. Materials leached from the trees may alter the growth of plants below. Tamm (1950) showed nutrient drip from trees increased the growth of moss round the edges of forest clearings. Allelopathic substances might also be washed from different species which could suppress growth of bramble below.

324. All the associations between tree canopy and bramble growth may only reflect the variations in root competition that are really controlling growth. Trenching experiments could perhaps separate these above and below ground competition factors. More work is clearly needed to separate or eliminate the different elements of tree competition and their effects on bramble growth.

CHEMICAL ANALYSIS OF MATERIAL FROM HARVEST PLOTS

MINERALS-MATERIALS AND METHODS

325 Material from the harvested plots was analysed for its content of nitrogen, potassium, phosphorus, magnesium and calcium. From changes in mineral concentrations inferences were drawn about the exchange of material between leaf and stem components. These were related to the simultaneous changes in growth.

MATERIAL

326 For each component, see page 22 , for each area, five samples were taken, each from a separate metre-square plot, after the material had been dried. Approximately 10g were taken for stem components, not all from the same section of stem, for leaves a handful. These were ground in a hammermill so as to pass a 1mm diameter sieve. The ground samples were stored in glass specimen tubes at room temperature.

327 ERRORS AND BIAS IN SAMPLING Allen (1974) recommends a finer grinding. Samples from the hammer mill were compared with more finely ground material from a ball mill, and with hand-ground samples all from the same original material. No significant differences were found in their mineral contents. There was no evidence for either contamination from the mill or of differential loss of minerals in the dust from the mill.

328 The material was not washed prior to it being dried. Some contamination by earth, insect droppings etc. could have occurred.

Obvious foreign material was removed during the sorting of components and the level of contamination was probably low.

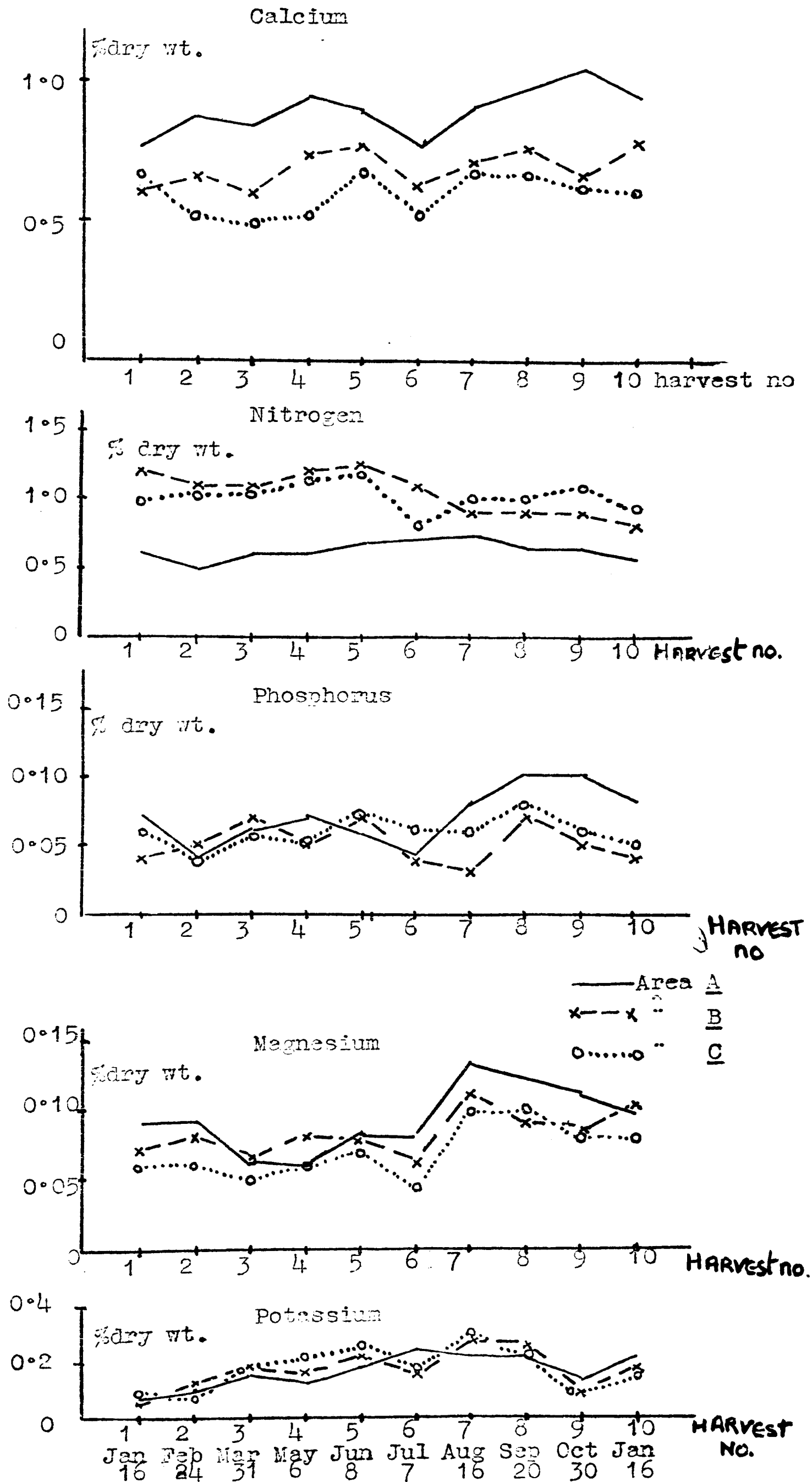
329 The sub-sampling procedure for each dried component resulted in the combination of material from the different rootstocks within a plot in any sample. Differences caused by plant-to-plant variation were thus reduced. Plots were harvested at different times of the day and it is assumed that diurnal fluctuations in mineral concentrations were small.

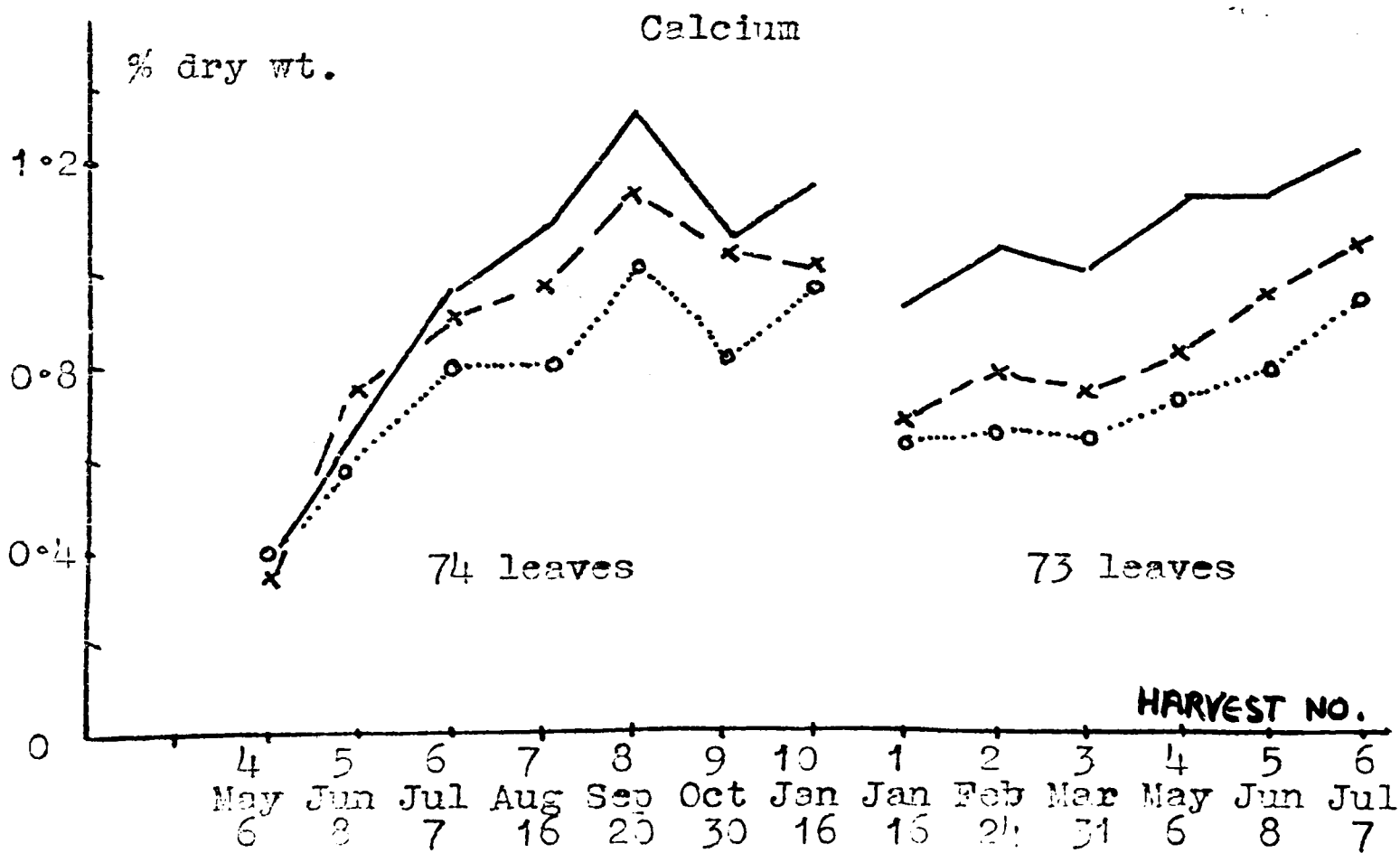
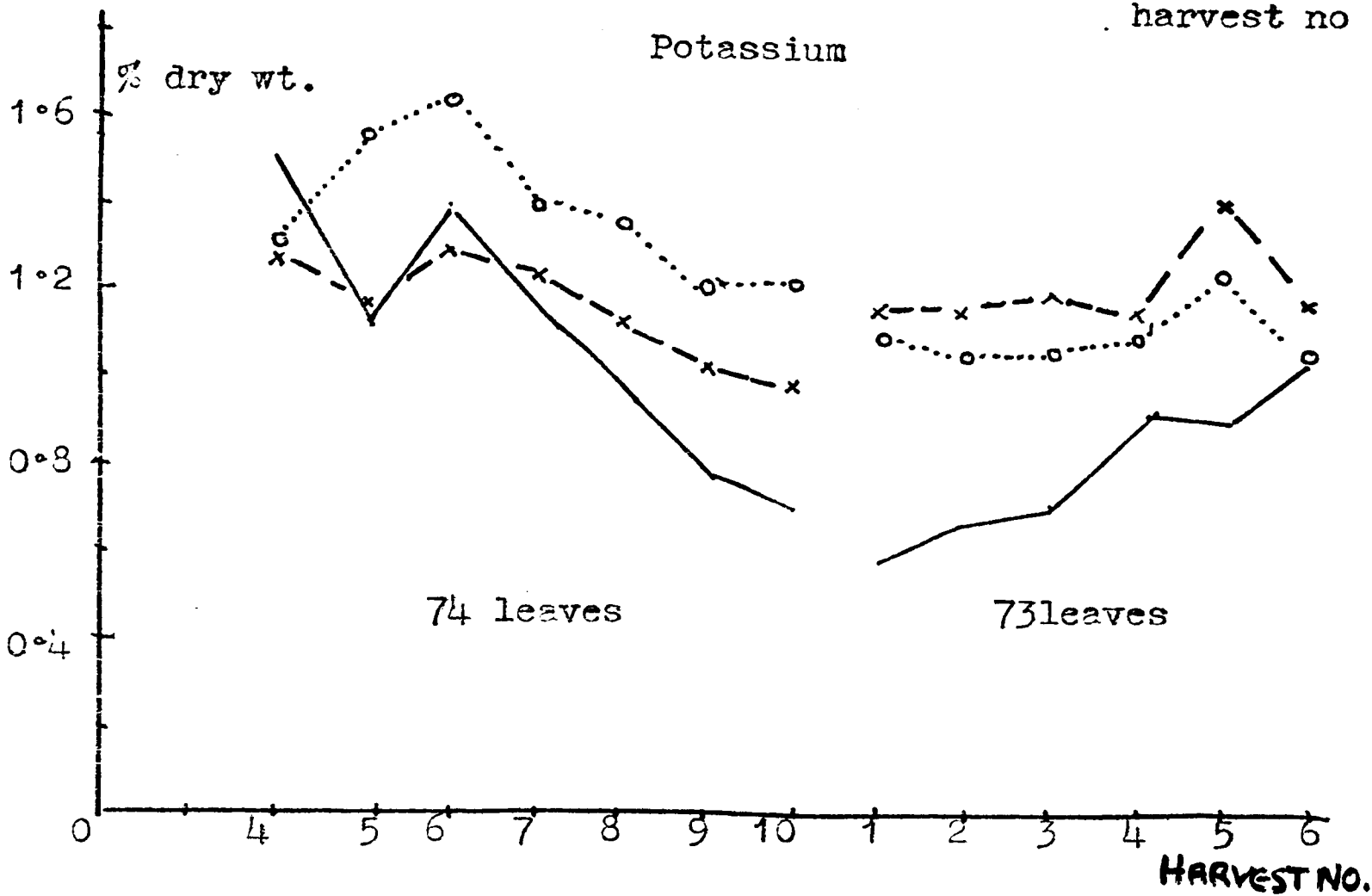
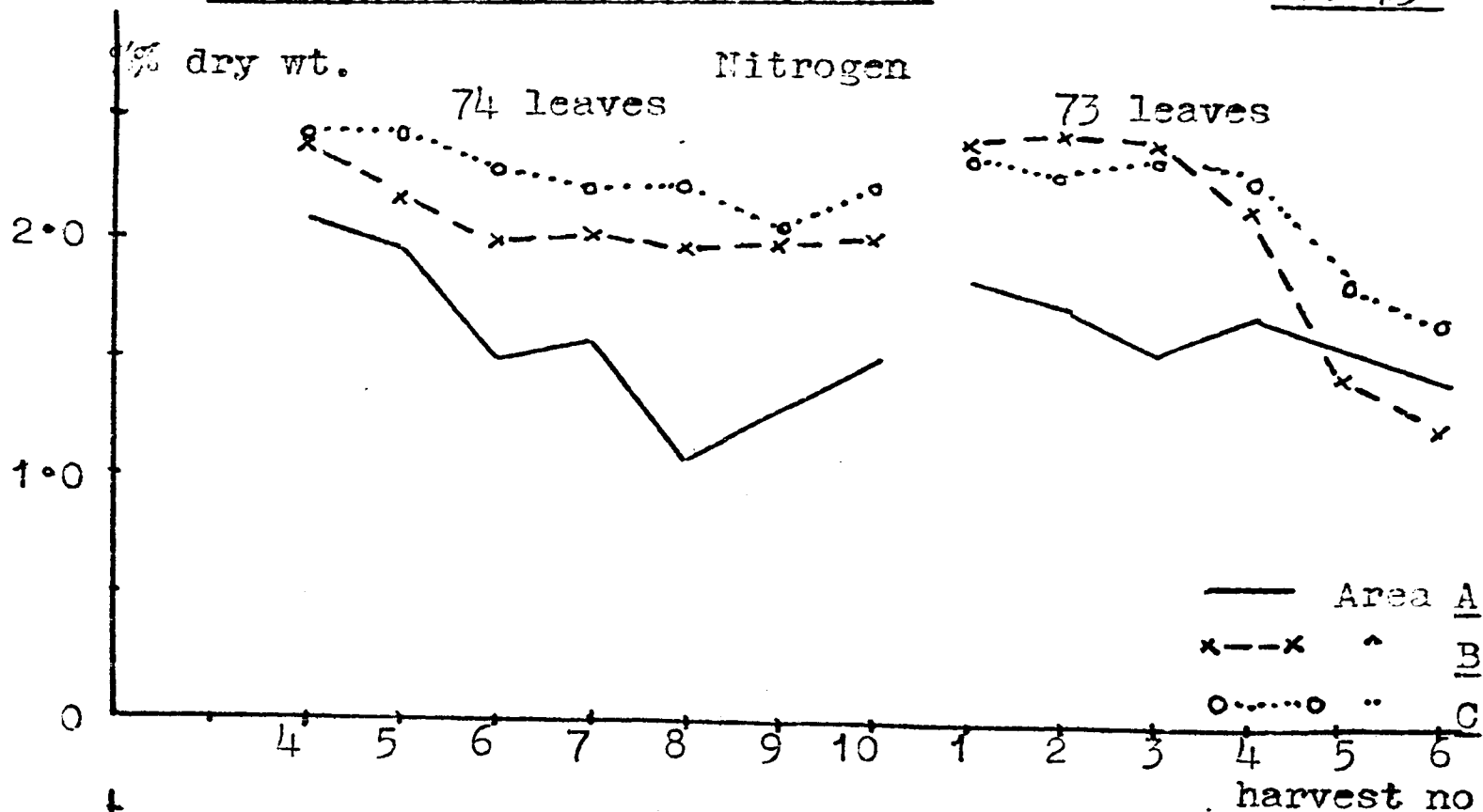
330 During die-back of canes, laterals and leaves, the proportion of the total amount of these components, present at maximum biomass, that was still alive, decreased. The samples for mineral analysis came only from the live fraction, the dead parts being included in the standing dead category. As die-back proceeded, therefore, the samples became increasingly atypical of the bulk of the original component that had been present the previous summer.

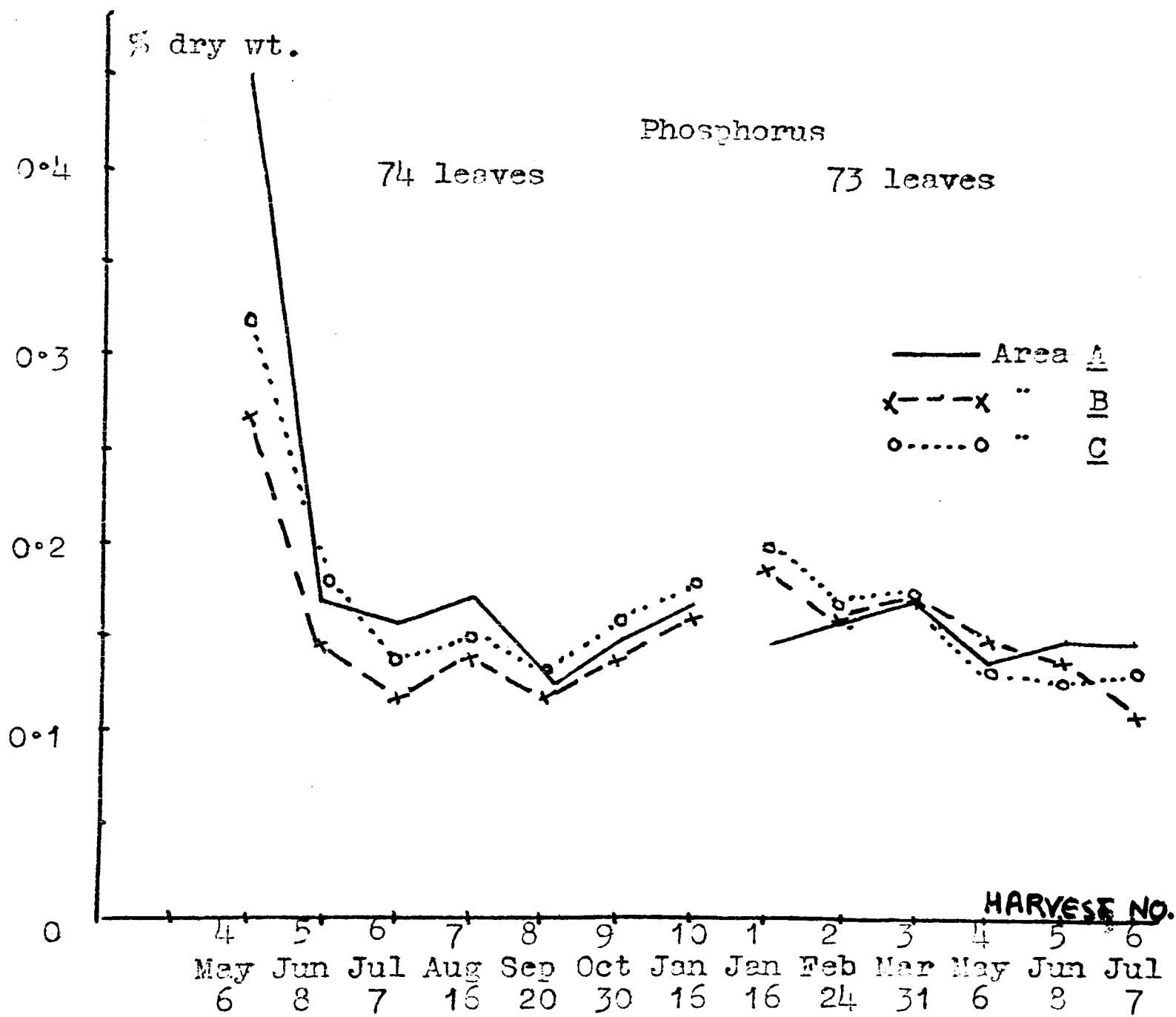
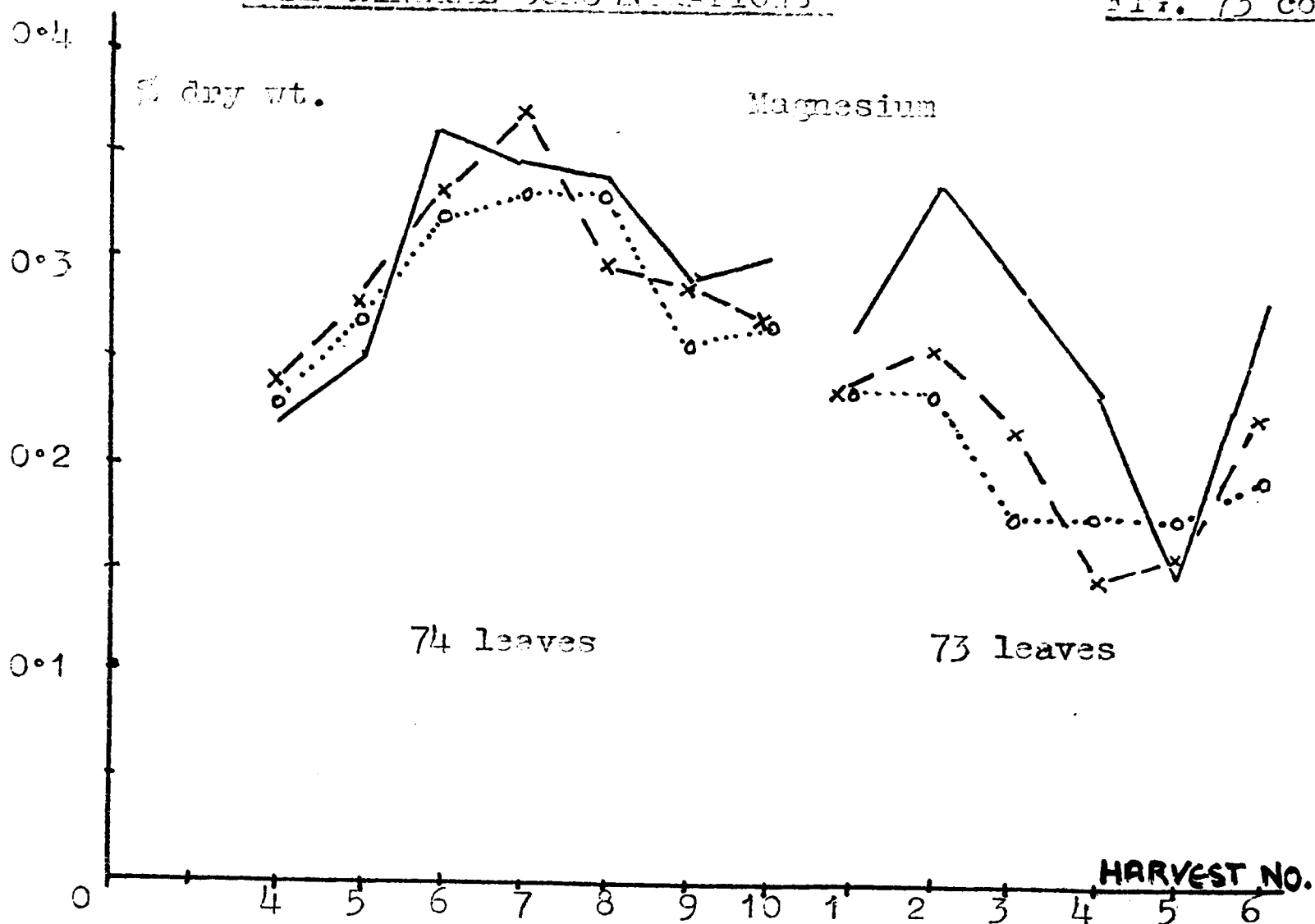
METHODS

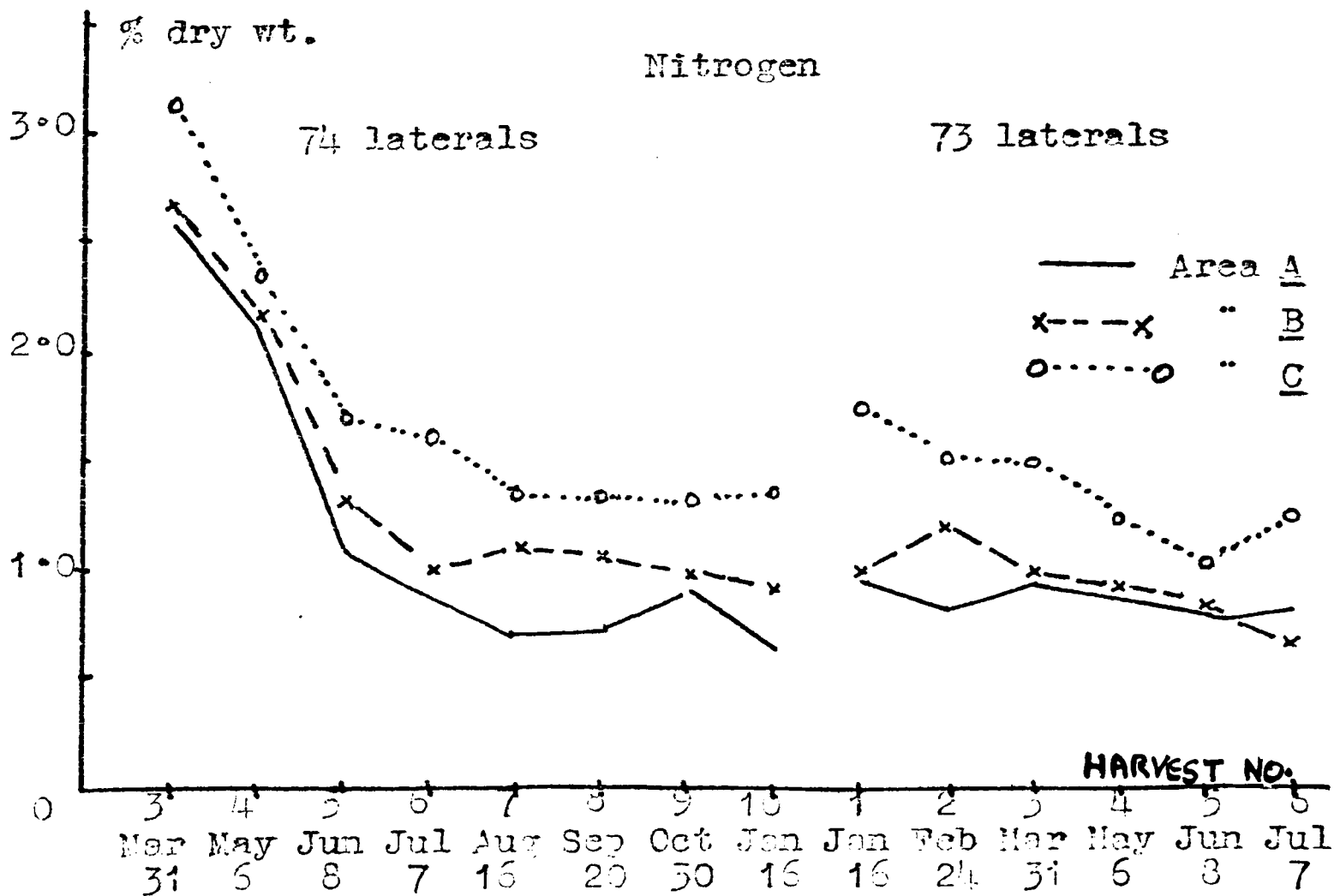
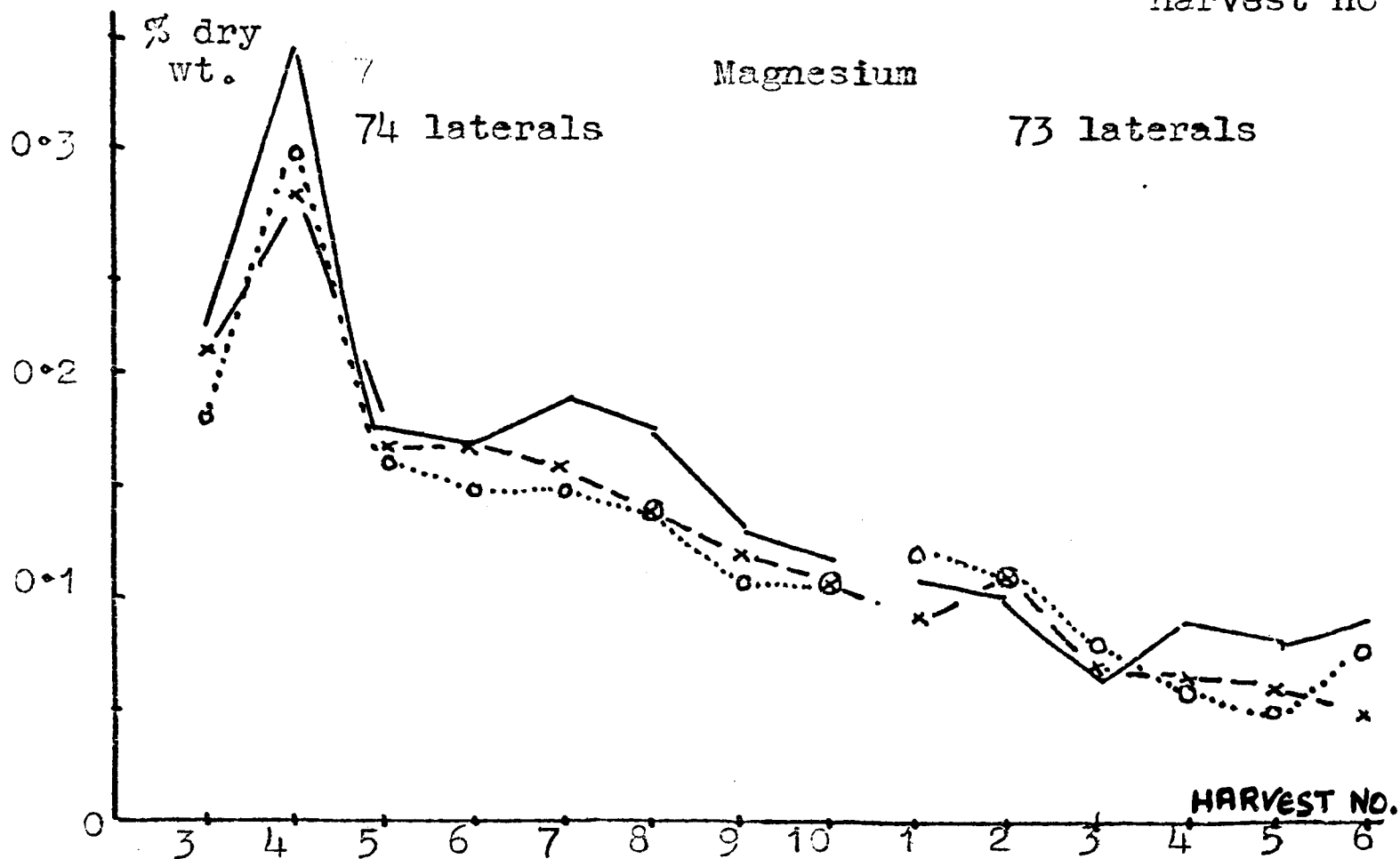
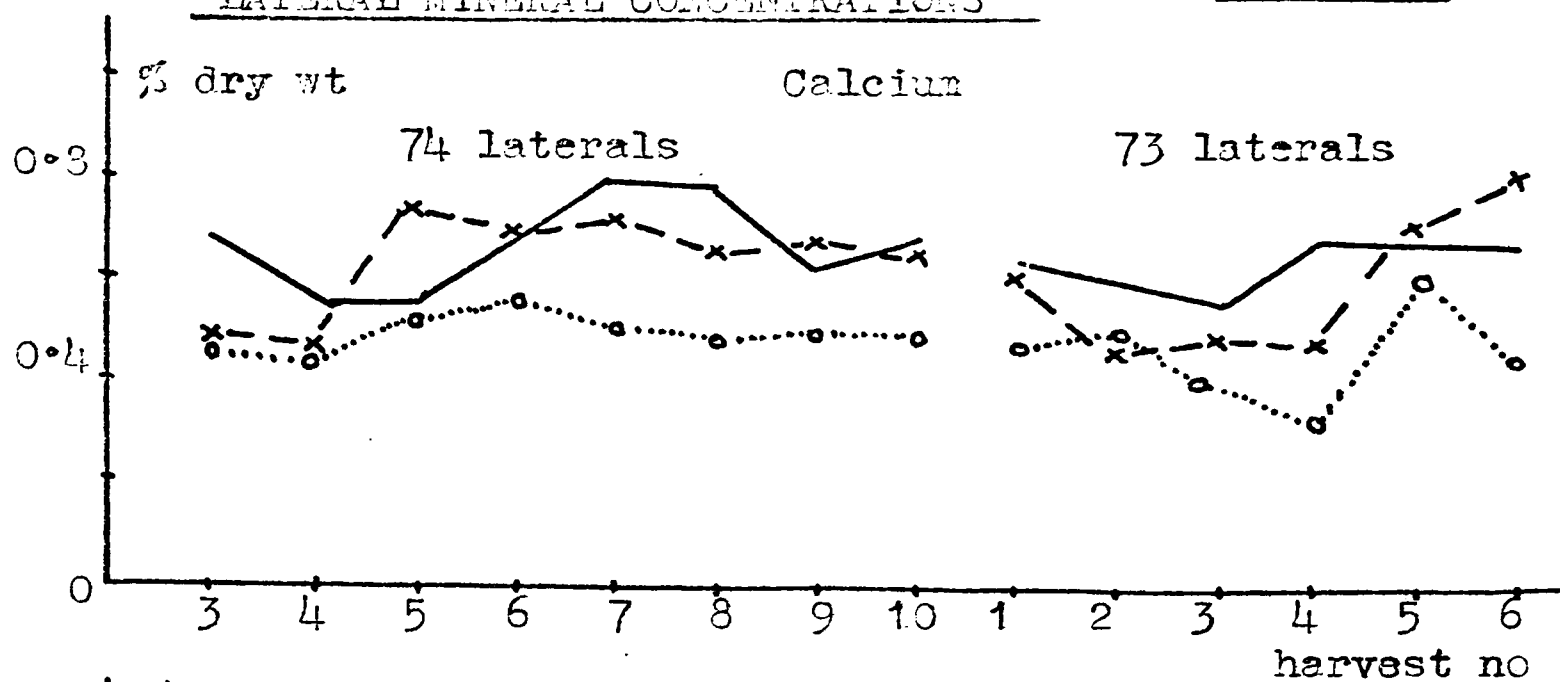
331 100 mg of ground material was dry-ashed in a muffle furnace overnight at 450^o, and the ash taken up in dilute nitric acid. From this solution potassium was determined by flame emission spectrophotometry, calcium and magnesium by flame absorption, on a Unicam. S.P.1900. Lanthanum chloride was used to suppress potassium interference in the calcium and magnesium determinations. Phosphate in the solution was determined by a variant of the vanado-molybdate yellow test (Jackson 1958). Precise details of the method used are given in Appendix I. A separate 50 mg of material was used for nitrogen analysis. Micro-Kjeldhal digestion using sulphuric acid and selenium catalysts was followed by the indophenol blue test. (Novozamsky 1974).

STANDING DEAD MINERAL CONCENTRATIONS









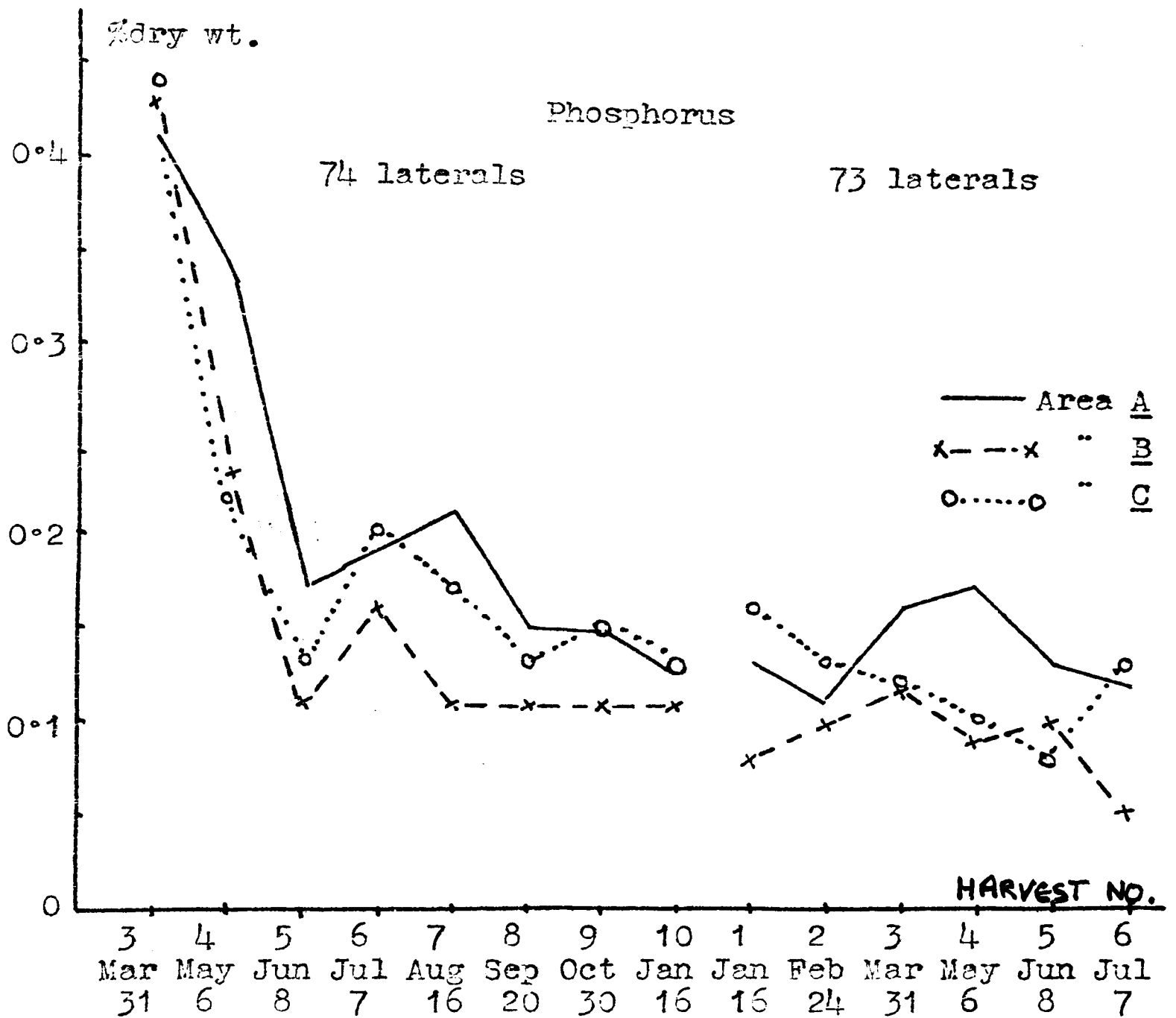
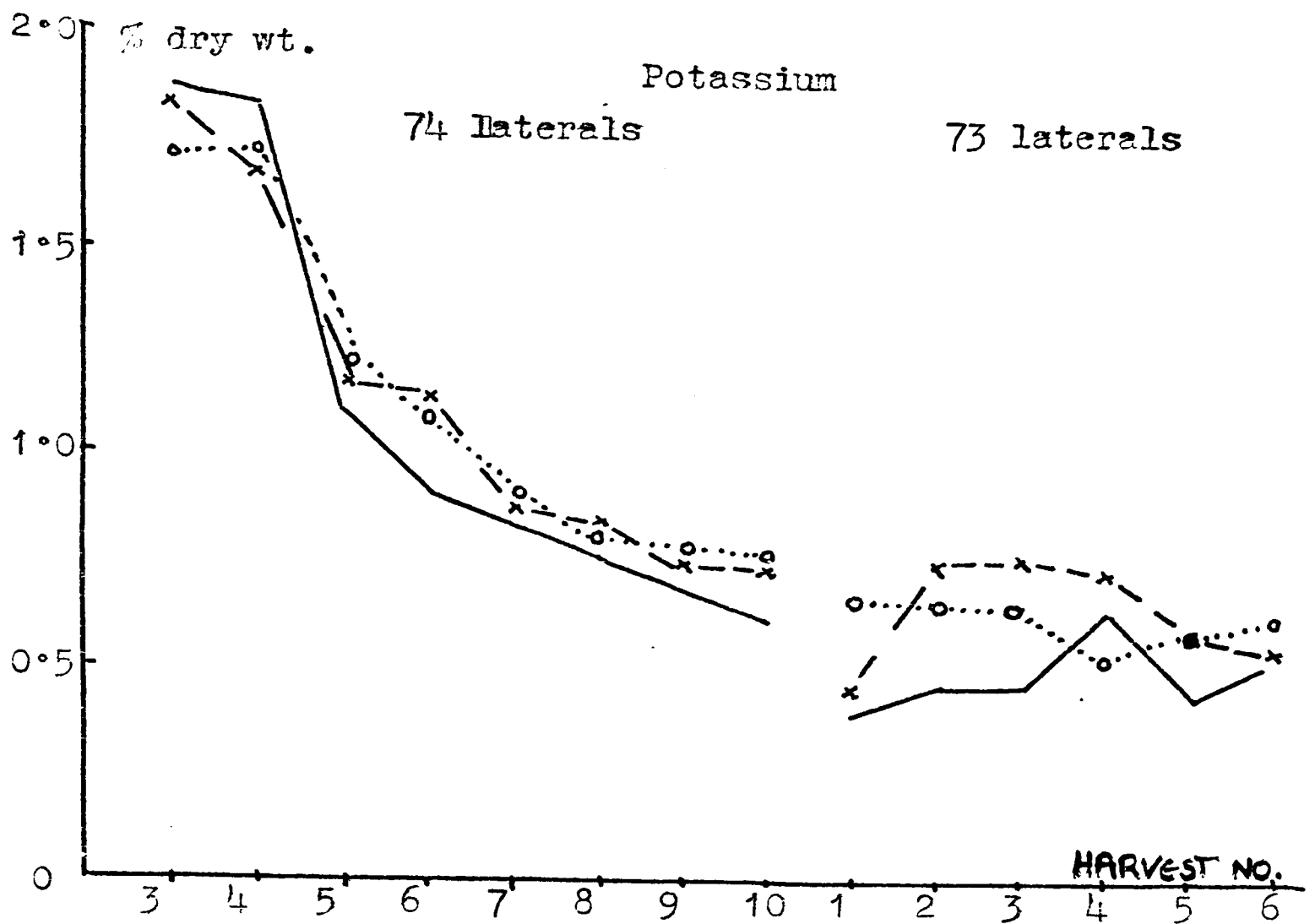


FIG 75

CANE MINERAL CONCENTRATIONS

Phosphorus

73 canes

72 canes

%dry wt.

74 canes

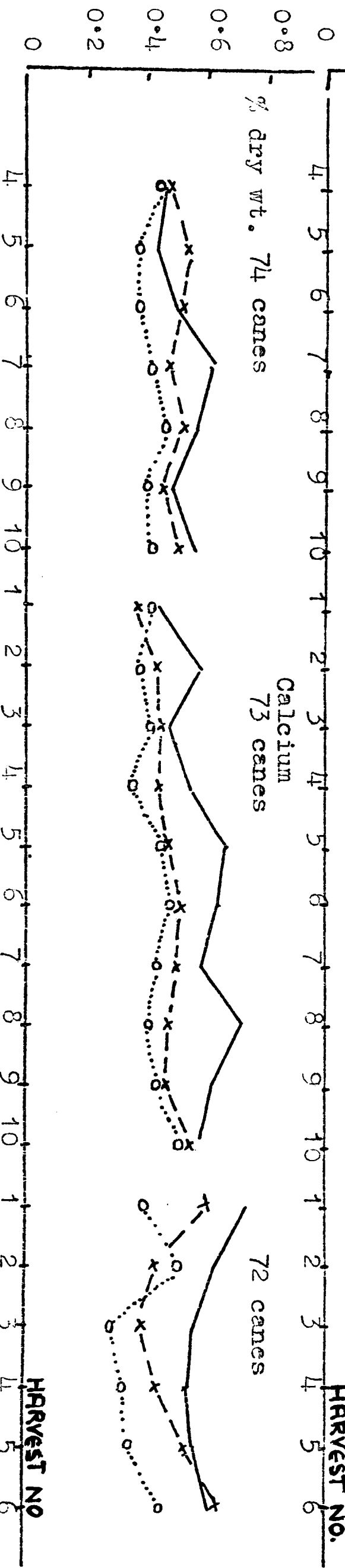
Area A
B
C

Calcium

73 canes

72 canes

% dry wt. 74 canes



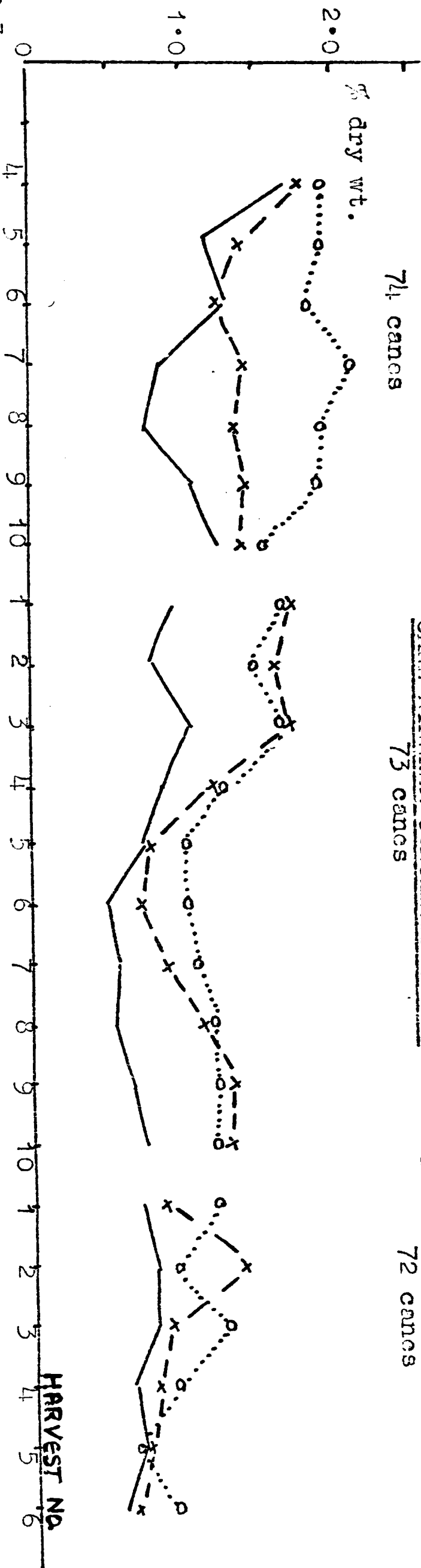
Jan 16 Feb 24 Mar 31 May 6 Jun 8 Jul 7 Aug 16 Sep 20 Oct 30 Jan 16

HARVEST NO

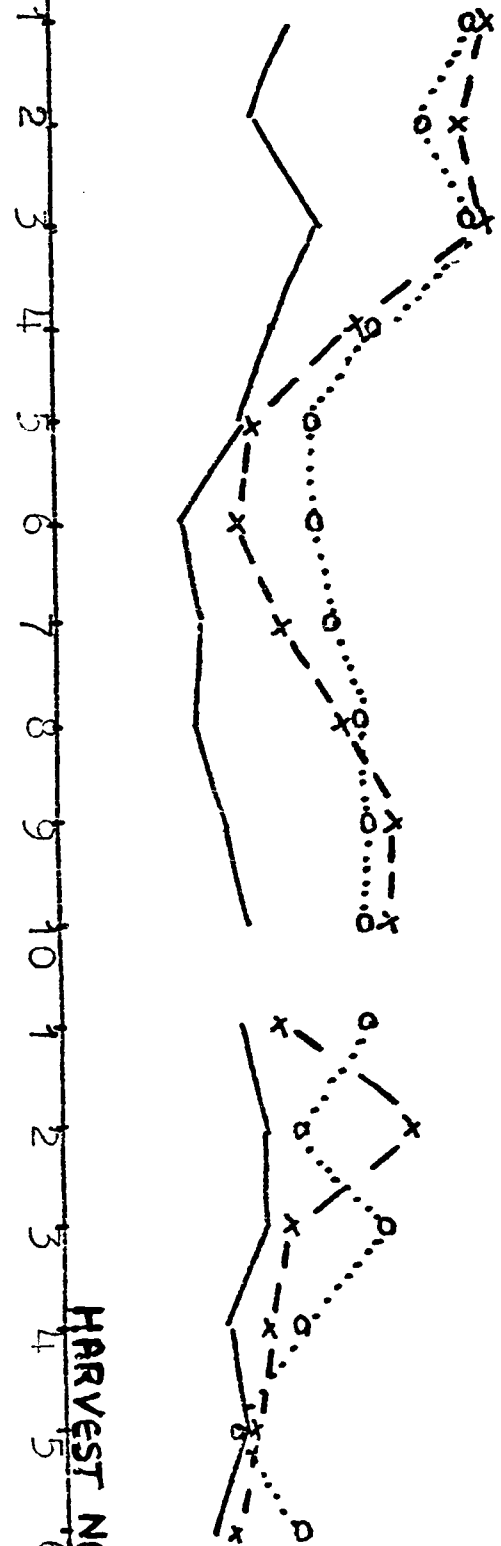
HARVEST NO.

CANE MINERAL CONCENTRATIONS - Nitrogen

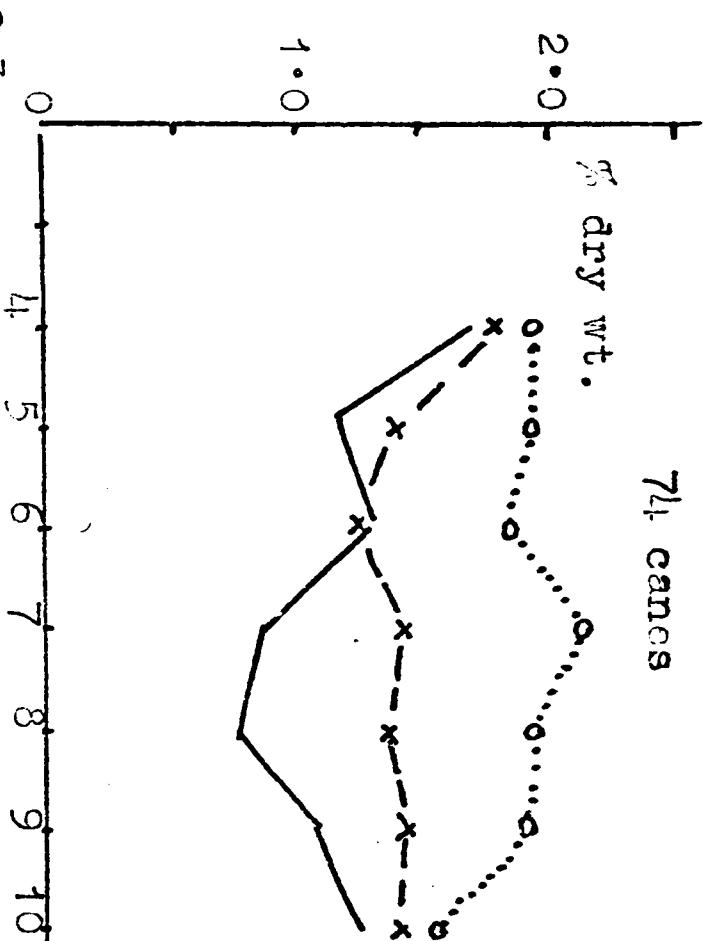
72 canes



73 canes

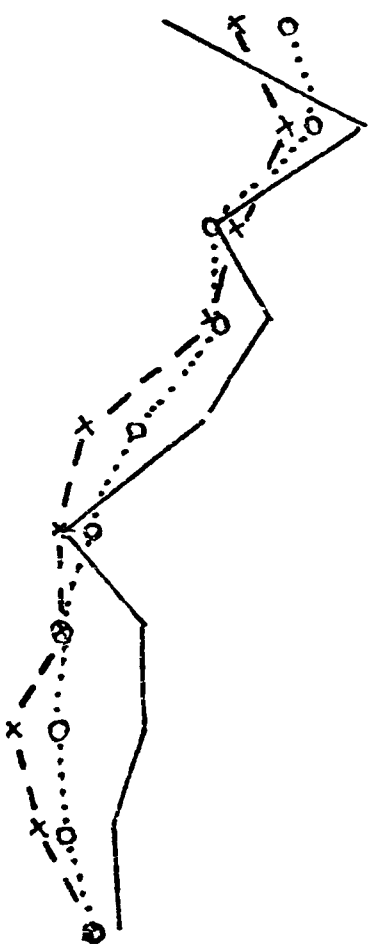


74 canes

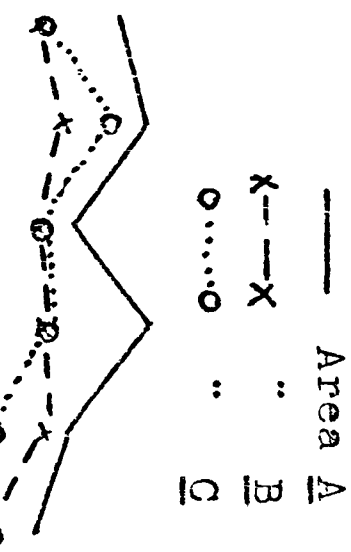


Magnesium

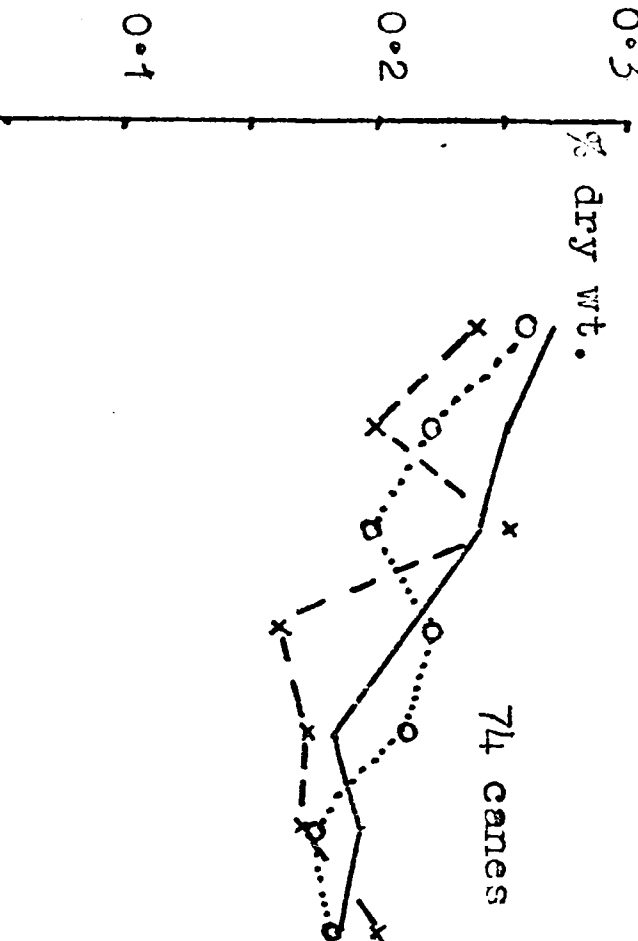
73 canes



72 canes



74 canes

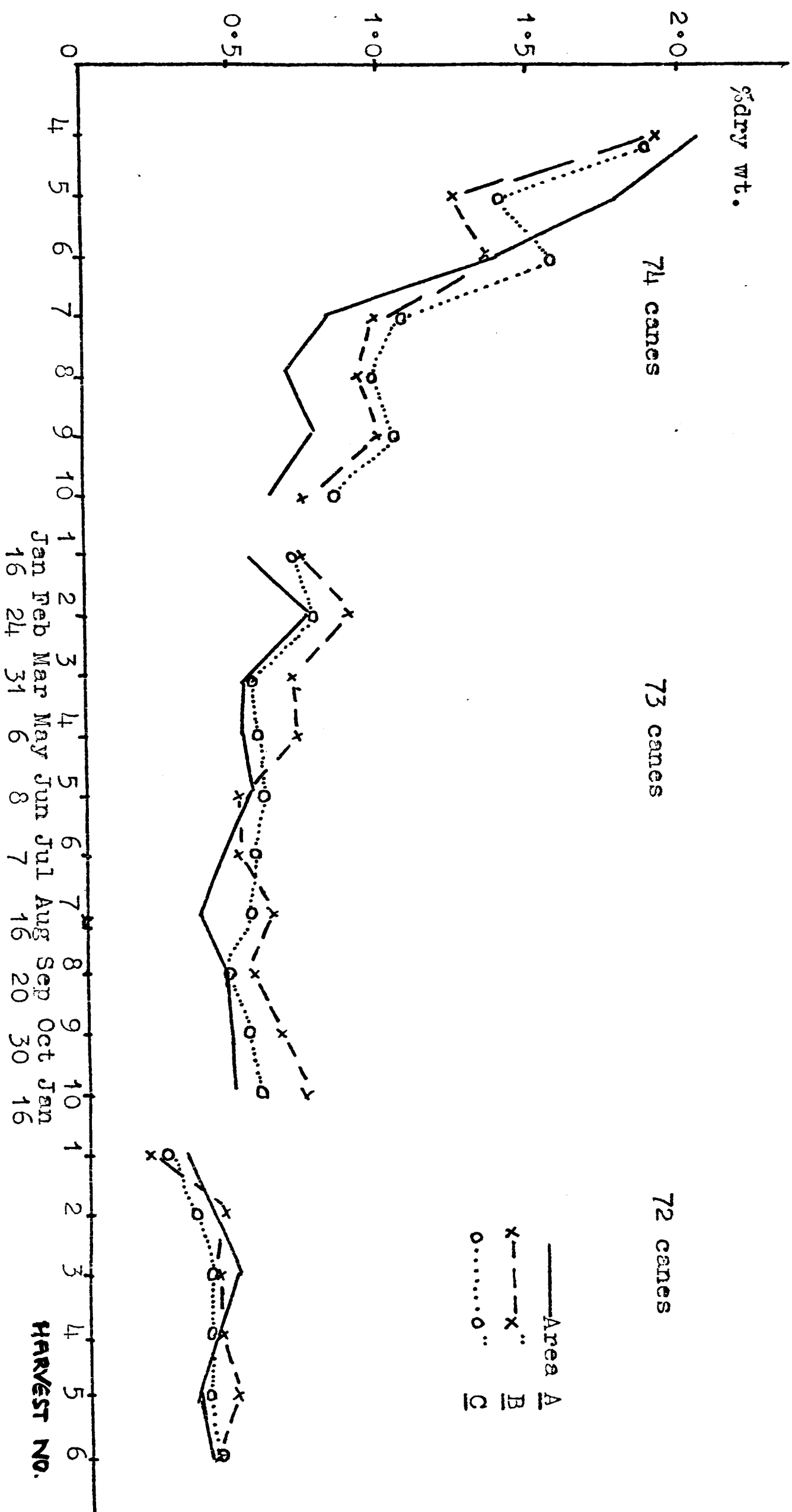


Area A
x---x B
o.....o C

Jan 16
Feb 24
Mar 31
May 6
Jun 8
Jul 7
Aug 16
Sep 20
Oct 30
Jan 16

HARVEST NO.

CANE MINERAL CONCENTRATIONS -- Potassium



332 REPLICATION Four replicates, for each component, for each harvest were used for the nitrogen analysis, each replicate being from a separate metre-square plot. Five replicates were used in the other analyses. Duplication of replicates was not carried out because differences between samples of the same component for the same harvest were greater than differences within a sample. Standard material was included in all batches of samples for analysis, as well as the usual reagent "blanks," to check for batch to batch variations in the analytical procedures. Material from the first analysis batches was re-analysed a year later to test for storage losses. These were not significant.

RESULTS - MINERAL CONCENTRATIONS

BETWEEN AREA DIFFERENCES

333 ^{P.200-207}
 Figures 72-75 show the changes in mineral concentration for different elements over the year. Many of the differences between the lines for the three areas are statistically significant. Each point, however, was based on only 5 x 100 mg samples per area (4x50 mg for nitrogen). Because field and sub-sampling errors were likely to be large compared to analytical errors, most of the differences between the areas in these figures were unlikely to be of biological significance. Over all components at all harvests, however, mean concentrations did show some fairly consistent differences between areas, the greatest being for nitrogen and calcium^{P.209} (Table 59).

334 ^{P.12}
 Area A had the highest soil pH (Table 4) and hence probably the greatest calcium availability. This was reflected in the higher calcium concentrations in the bramble. The heavier soil in A probably had a higher nutrient availability generally. Potassium and nitrogen levels were, however, lower in A than in B or C. The greater carbo-

TABLE 59

DIFFERENCES IN MEAN MINERAL
CONCENTRATIONS BETWEEN A,B,C.

For most components at most harvests

Area A had the highest concentrations
of Ca, P, Mg.

the lowest concentrations
of K, N.

Area B had the lowest concentrations
of P.

Area C had the highest concentrations
of N.

the lowest concentrations
of Ca.

There was little difference between areas B and C in the concentrations of either K, or Mg.

TABLE 60

PHOSPHORUS CONCENTRATIONS IN
BRAMBLE FROM AREA D

Samples collected July 9th 1975

	Area A	B	D	% dry weight	P
Second year canes	0.12	0.14	0.05	"	"
Laterals	0.23	0.22	0.09	"	"
Leaves	0.19	0.18	0.08	"	"

hydrate production in A, in particular the greater amounts of woody tissue in the stems, "diluted" additional uptake of these minerals relative to B and C.

335 There was no extensive analysis of material from area D, the least productive of all the Wytham areas studied. The few samples that were analysed, however, showed very low phosphorus levels (P.209 Table 60). As this is one of the three elements, most abundant in A the area of highest growth, it is possible that it is limiting growth in some areas of the wood.

VARIATIONS BETWEEN COMPONENTS IN THE AREA DIFFERENCES

336 STANDING DEAD Differences in the concentrations of phosphorus and potassium between areas were markedly less than for live stem components. Differences for the dead between areas were also slightly less for nitrogen and magnesium, but the calcium differences between standing dead in A, B and C were as great as for the live stem components. After death leaching of cell contents occurs and potassium, particularly, was likely to be lost, reducing the differences between areas. The bulk of the calcium, however was present in the cell walls as insoluble pectates. The differences between areas were thus maintained.

337 NEW GROWTH IN A Growth started later in the spring in A than in B or C and this effect was still apparent in dry weight per unit area at harvest 6. Up to this time therefore, new growth in A (74 canes, 74 laterals, 74 leaves) was relatively younger than the equivalent components in B or C, harvested on the same date. This was reflected in the potassium level for these three components. Potassium concentrations fell with age, so the A components being younger had relatively higher potassium concentrations than B or C. This partially off set the overall tendency for potassium concentrations to be lower in area A.

338 The same was found for calcium concentrations in 74 leaves where concentrations for A were relatively lower at the early harvests when calcium concentrations were rising. Lower calcium levels in 74 canes and higher phosphorus concentrations for 74 leaves and canes at H4 were probably also caused by the later start to growth in A relative to B or C.

339 DIE-BACK At the other end of the life-cycle, survival into the third-year was greatest in A and various of its canes produced "tertiary," laterals. Higher concentrations of magnesium and phosphorus particularly, were found compared to B and C where die-back was more advanced. This is consistent with withdrawal of nutrients prior to the death of stems.

SEASONAL CONCENTRATION CHANGES FOR COMPONENTS

340 In the following discussion of seasonal changes for the different components, results from all three areas have been combined. (P. 212-215) (Figures 76-80). The leaf curves on the figures are those for lateral leaves as most of the 74 leaf samples were from laterals. Where cane leaves were analysed no difference was found and for 73 leaves no separation at all was made. A similarly shaped curve could therefore be drawn in at the appropriate place for the leaves on the first-year canes, but has been left out for simplicity.

GROWTH OF YOUNG STEMS

341 FALLS IN NITROGEN, PHOSPHORUS, POTASSIUM During development of young canes or laterals, the proportion of their total weight made up by the growing point decreases as the amount of woody, conducting

Fig 75

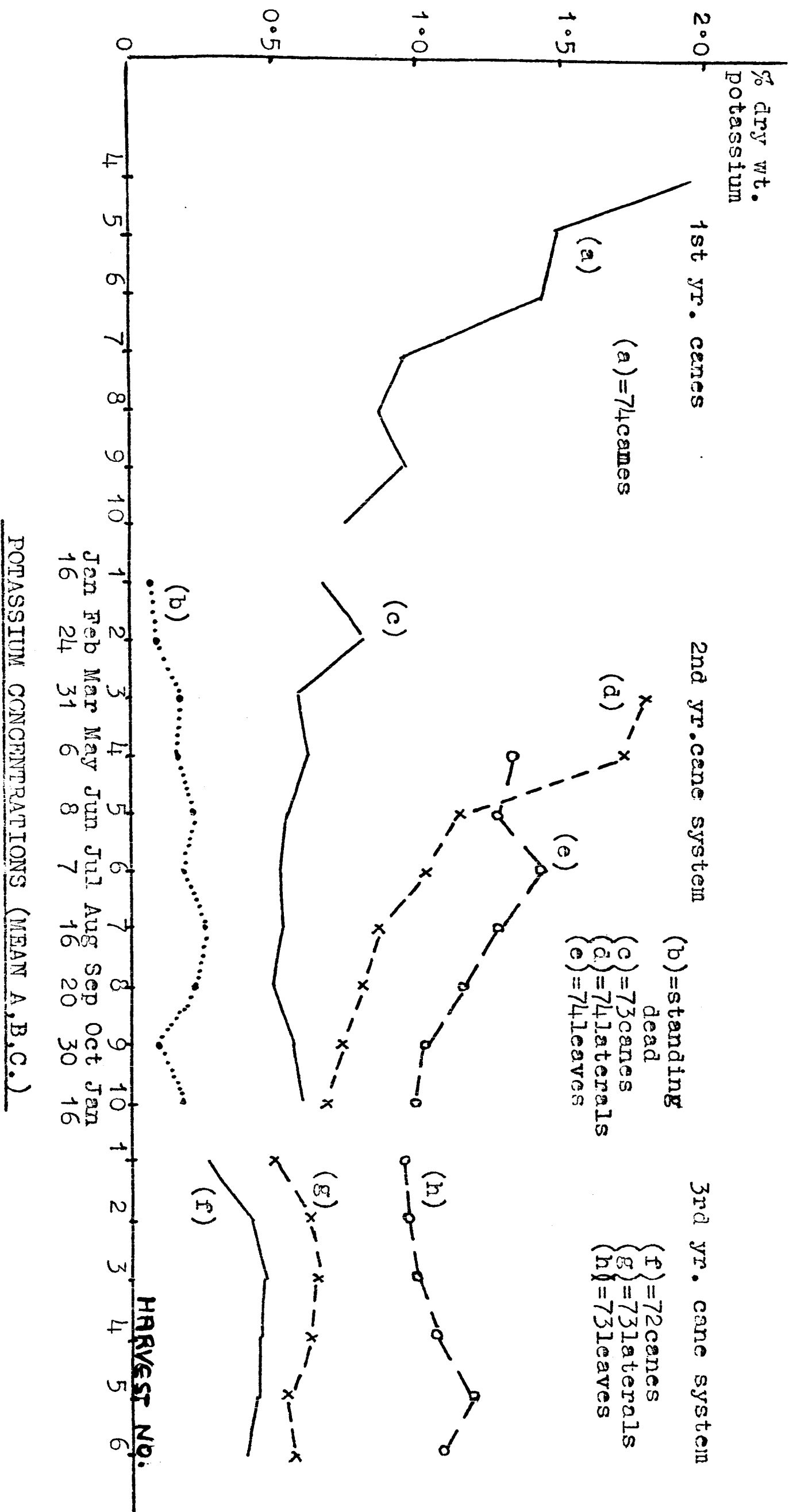
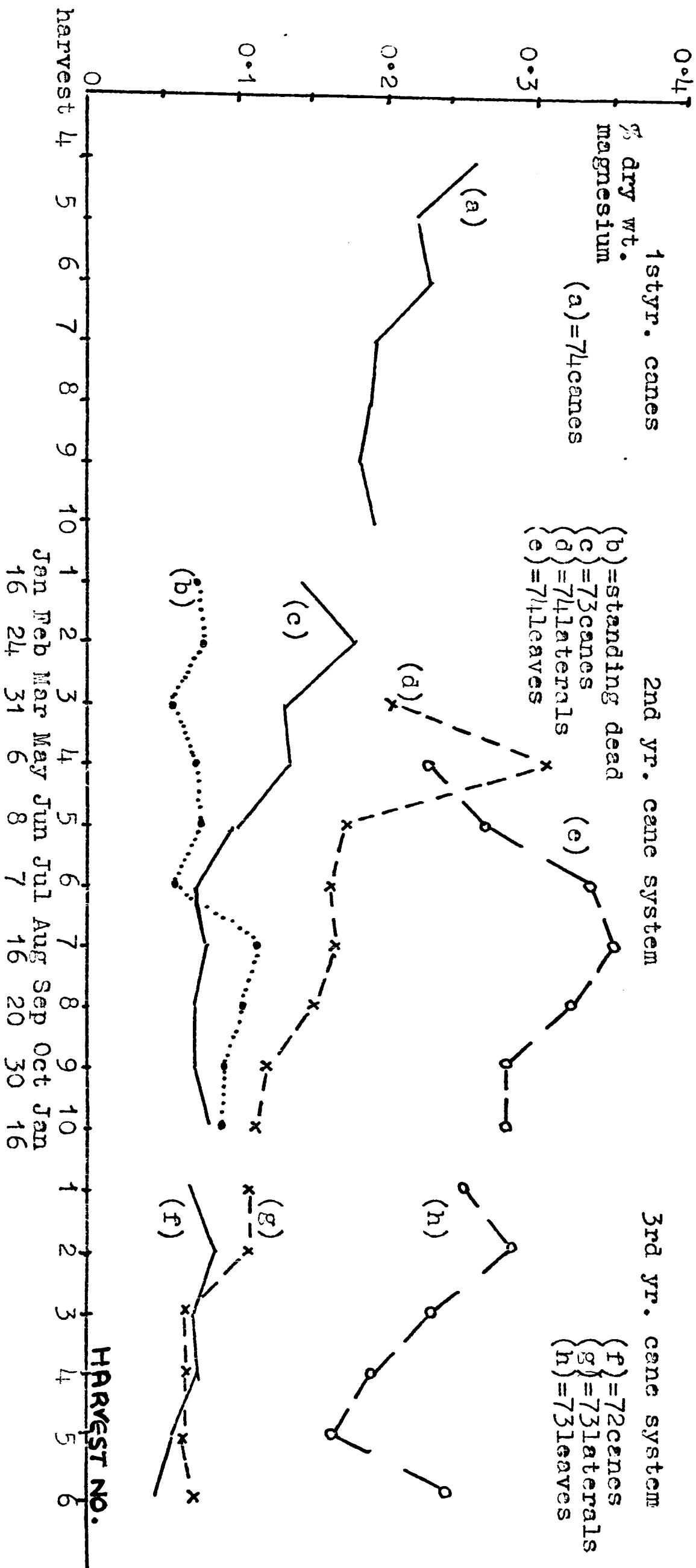


FIG 77



MAGNESIUM CONCENTRATIONS (MEAN A, B, C.)

FIG 79

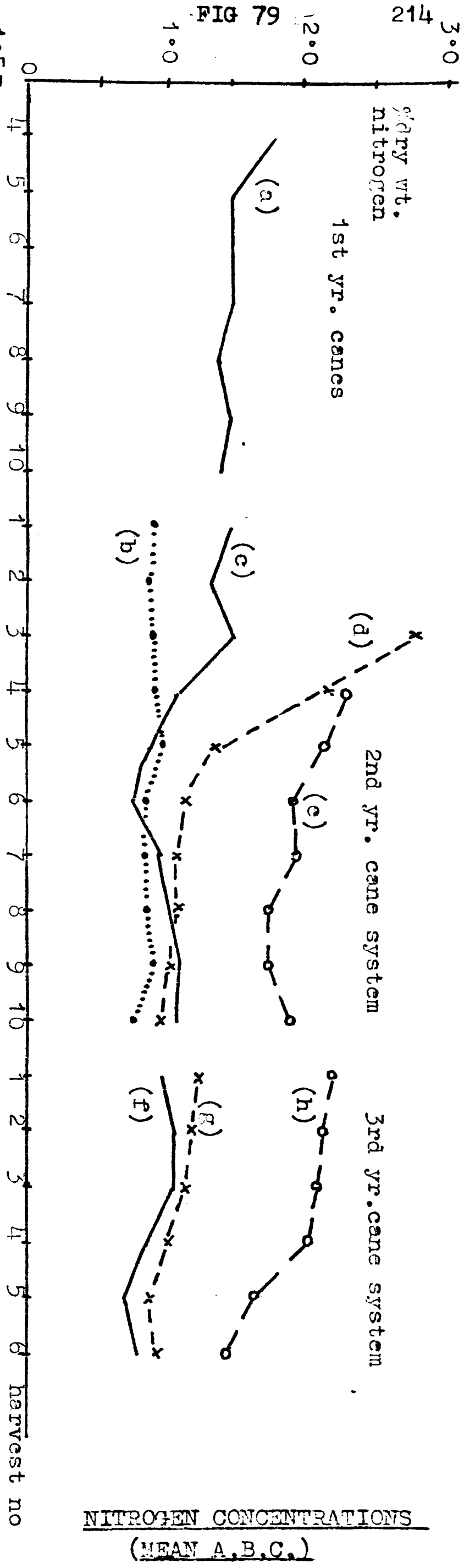
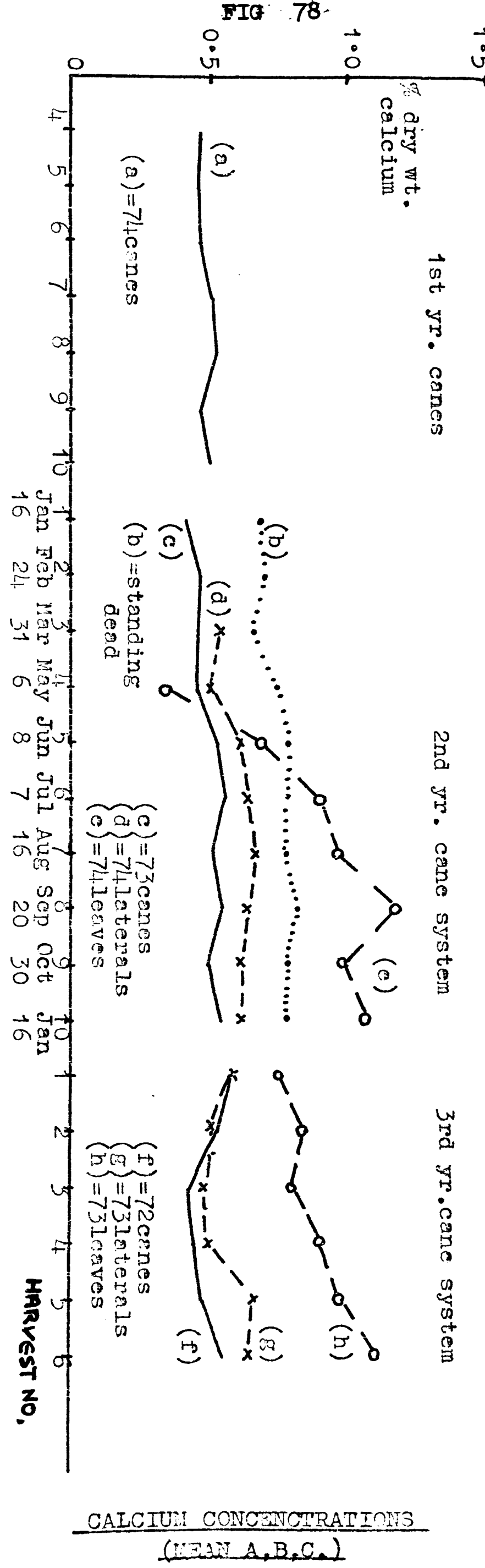
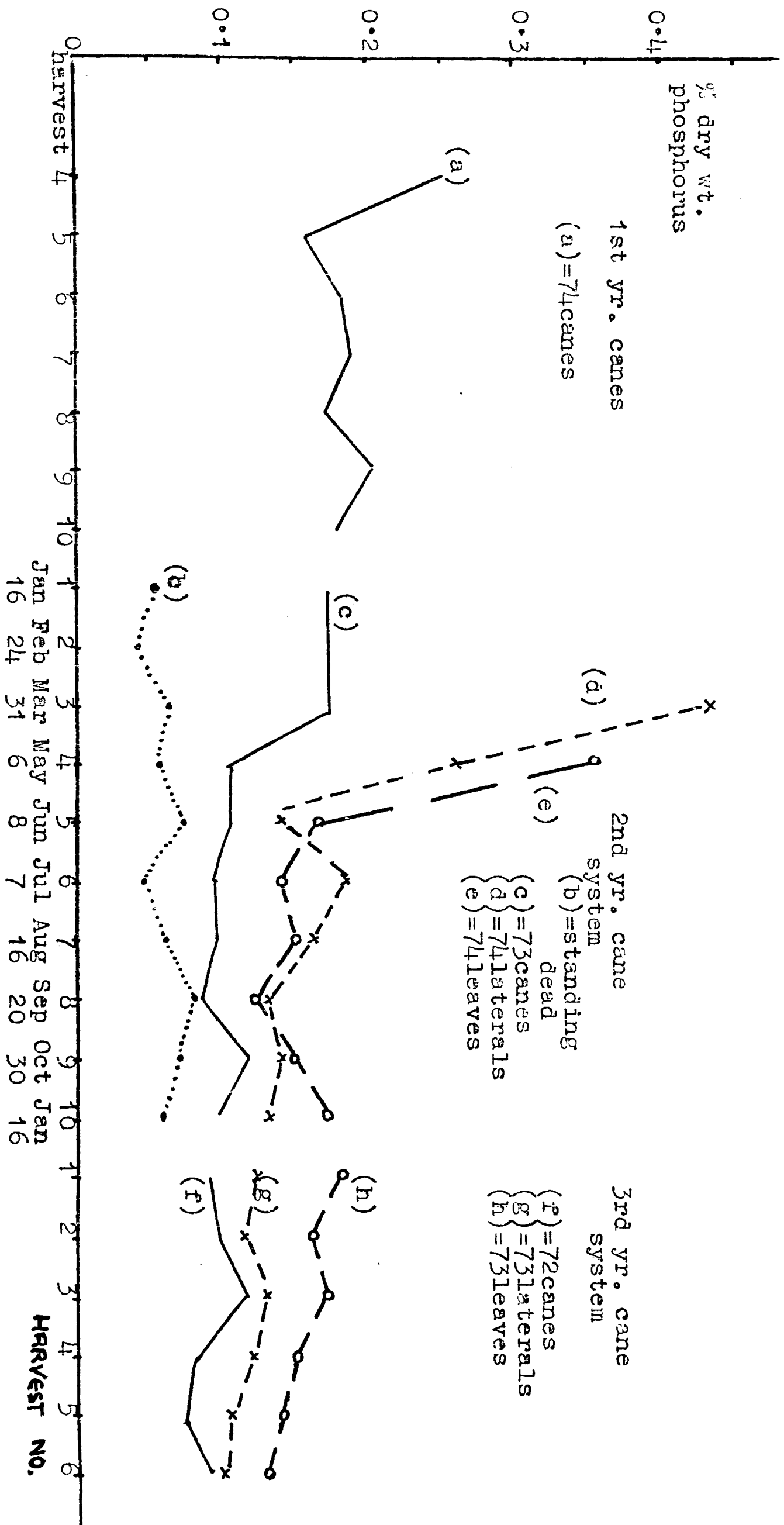


FIG 78



HARVEST NO.

FIG 80



PHOSPHORUS CONCENTRATIONS (MEAN A.B.C.)

tissue increases. The former tissue is much higher in minerals than the latter. There were, therefore, steep falls in the concentrations of nitrogen, phosphorus and potassium during stem growth.

342 The falls in the cane concentrations of nitrogen and phosphorus were less than for the laterals. The young 74 canes were relatively older than the laterals when they were first separated, see page 30 . The initial measured concentrations were thus lower and the fall in concentration as the stems grew, less pronounced. Potassium levels remained high for a longer period in the growth of young stems, to judge by the laterals, so that high initial concentrations were also found for this element in the canes.

343 MAGNESIUM IN YOUNG STEMS Magnesium showed a small decline in concentration during first-year cane growth. Much of the magnesium in the cane was probably in the outer layers as chlorophyll and its precursors. In the young laterals a sharp peak in magnesium concentrations occurred immediately before the main period of leaf expansion, some of this magnesium being transferred to the developing leaves.

344 CALCIUM IN STEMS Alone among the five elements studied, calcium showed no great changes in concentration during the entire life of the stems. Calcium is not associated particularly with meristems or young growth. The bulk of it was in cell walls and uptake of calcium more or less matched stem growth.

MINERALS IN THE SECOND-YEAR CANE SYSTEM

345 TRANSFER FROM CANES TO LATERALS From H3 - H6 there was a sharp fall in the concentrations of nitrogen, phosphorus and magnesium,

coinciding with the growth of the laterals. The main transfer of minerals, indicated by these concentration falls, was after H3. The minerals must, therefore, have been stored in the canes themselves rather than in the buds, because the latter were separated from the canes at H3. Potassium levels over this period, by contrast showed only a very slight fall.

346 The storage of nitrogen and phosphorus may have contributed to the lower falls in the concentration of these elements, relative to laterals, during first-year growth. (see also page 2/6). Storage of minerals kept the concentrations higher in full grown canes than in full-grown laterals as compared to potassium, where no storage occurred and the final concentrations in canes and laterals were similar.

347 SUMMER PHOSPHORUS PEAK IN LATERALS There was a burst of meristematic activity in the laterals in mid-summer, associated with flower and fruit production. There was a corresponding rise in the concentration of phosphorus in the laterals at this time.

LEAF CONCENTRATION CHANGES

348 74 LEAVES Calcium is not very mobile in the phloem. As a result calcium transferred to the leaves, by the transpiration stream accumulated in them. Unlike stems, therefore, leaves showed a marked rise in calcium over the season. There was also a build up of magnesium in the leaves during leaf expansion and the formation of chlorophyll. The magnesium concentrations fell again in the autumn, however, when some leaves were dying off. There may have been withdrawal of some magnesium prior to death of the leaves.

349 Potassium and nitrogen leaf-concentrations fell much less

during growth than did the stem concentrations. Leaf expansion was matched by further uptake of these minerals and the leaves did not contain the large amounts of woody tissue found in the stems. The concentration falls in the later part of the year as with magnesium, occurred during the dying-off of leaves. Uptake of phosphorus into the expanding leaves was slower than for the other elements and levels fell sharply. Subsequently, however, there was little change and no sign of a decline in concentrations in the autumn.

350 73 LEAVES The decline in nitrogen and magnesium concentrations, started in 74 leaves in the autumn, continued when die-back started again in spring and early summer. Leaf phosphorus also declined slightly suggesting withdrawal of minerals from the old leaves. Potassium and calcium levels rose, however, during the early summer. Part of this rise may have been caused by loss of dry weight from the leaf during senescence rather than by further accumulation of minerals in the leaves. This would mean that the declines in concentration of phosphorus, nitrogen and magnesium underestimate the amount of withdrawal that took place.

351 There was, for an unknown reason, a sharp rise in the magnesium concentration of the 73 leaves not shown by the other elements at harvest 6. Possibly the leaves from which this sample was derived, were particularly vigorous and magnesium withdrawal not as far advanced as in previous samples. By harvest 6 the leaf weight^{was} less than 30% of that at the beginning of the year so that these leaves were very atypical of the 73 leaves originally formed.

TRANSITION FROM LIVE CANES TO STANDING DEAD

352 There was little evidence, from concentration changes, for withdrawal of material from canes and laterals in the third-year. By this time, however, the concentrations in these stems were little

different from those in the standing dead. For nitrogen, phosphorus, magnesium, potassium the transition from live to dead stems involved a reduction in concentration. Calcium levels were higher in the standing dead than in live stem components. This increase was caused by a loss of dry weight from the standing dead rather than by any further uptake of calcium. Thus some loss of the other minerals must have occurred to match this loss of dry weight. It was impossible to tell whether the final changes in mineral content and dry weight associated with death of stems occurred by rapid withdrawal immediately prior to death, or by leaching and the activity of micro-organisms shortly after death.

353 CHANGES IN STANDING DEAD OVER THE SEASON During the year there was no change in the weight of the standing dead and little change in its chemical composition. There were small rises in magnesium, potassium and phosphorus concentrations in the autumn. At this time there was an influx of dead inflorescences, some leaves and small laterals. Although these had little effect on the weight of the standing dead, they had a relatively high mineral content.

YEAR-TO-YEAR VARIATION

355 Differences in mineral concentrations between equivalent components at the beginning and end of the year were small. The greatest were for calcium, between 74 and 73 leaves, and potassium, 73 and 72 canes. This latter could have been some systematic error, as there was quite a large difference between 74 and 73 laterals potassium concentrations also.

FIG 81

COMPARISON OF MINERAL COMPOSITION OF
OAK AND BRAMBLE TISSUES

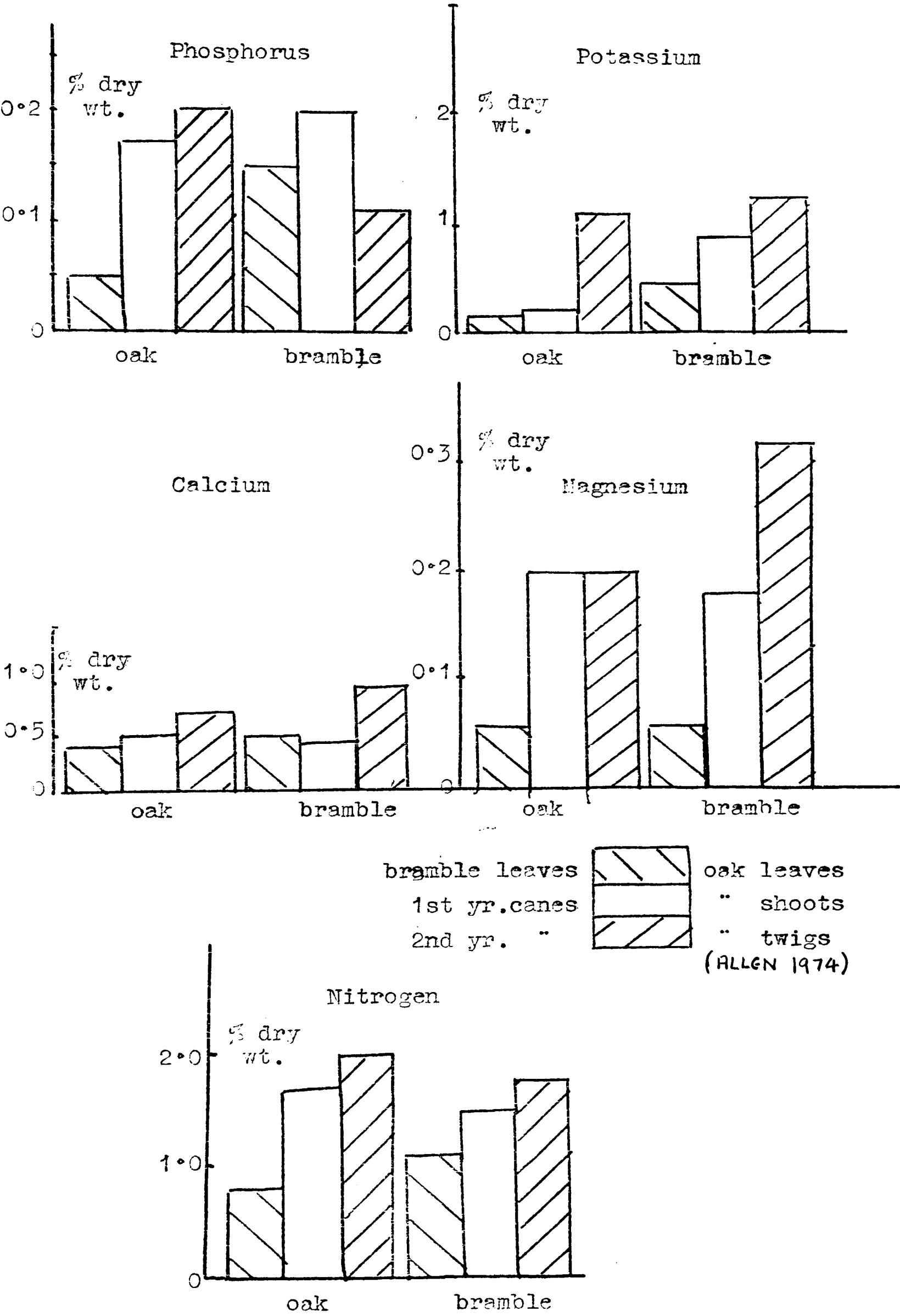


TABLE 61

MINERAL CONTENT OF BRAMBLE
% DRY WEIGHT

	N	P	K	Ca	Mg	Source
Leaves	2.2	0.19	1.3	1.2	0.25	Allen (1974)
	1.8	0.15	1.2	1.3	0.36	Madgwick (1965)
	2.5	0.15	1.5	1.1	0.43	Duvigneaux (1967)
Stems	0.6	0.09	0.7	0.5	0.13	Madgwick
	1.0	0.10	1.0	0.6	0.40	Duvigneaux

TABLE 62

MINERAL CONTENT OF ABOVE GROUND
BRAMBLE BIOMASS

Element	Area	Winter			Summer			
		A	B	C	A	B	C	
P		343	246	133	563	377	207	mg/sq.m
Mg		381	286	158	840	490	259	"
Ca		1490	998	586	2746	1988	905	"
K		1592	1171	663	3671	2979	1481	"
N		3479	2506	1408	5513	3818	2183	"

Mineral content of undergrowth from
under various hardwood stands
(Ovington 1956)

Summer		
P	24 - 386	mg/sq.m
Mg	21 - 515	"
Ca	57 - 4616	"
K	233 - 2297	"
N	200 - 5000	"

COMPARISON WITH RESULTS FROM OTHER SITES

355 Mineral concentrations have been reported previously for
 bramble, generally for material collected in the summer(^{P.221} Table 61) Most
 of the values are similar to those found here. The stem value for
 nitrogen of Madgwick is low compared to those for Wytham and the
 magnesium values of ^{P.220} Duvigneaux high. Figure 81, compares concentrations
 in first-year canes, second-year canes and leaves, with those in oak
 twigs, new shoots and leaves. These bear a similar age relation to
 each other as for the bramble components.

TOTAL WEIGHTS OF MINERAL IN ABOVE-GROUND

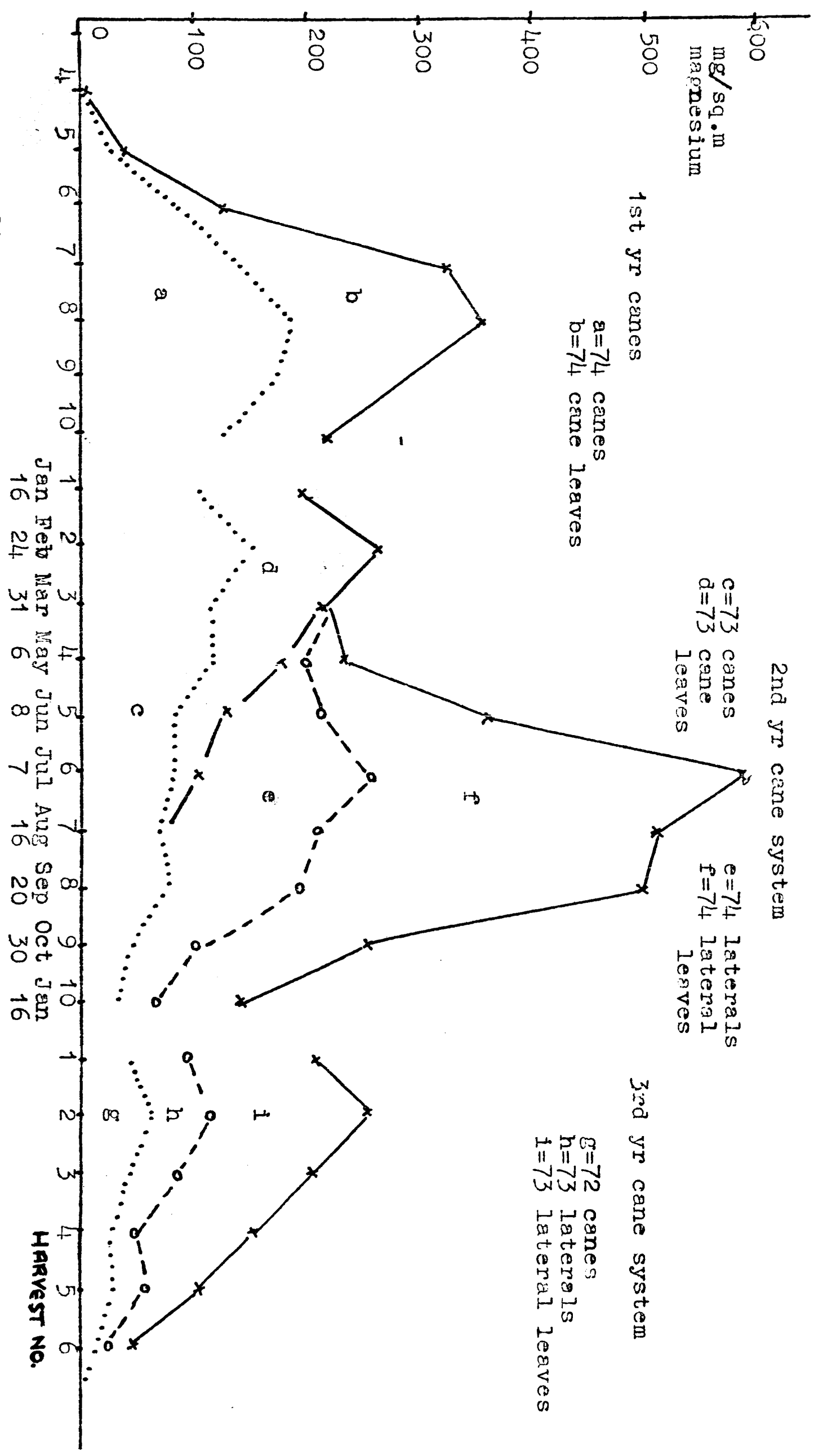
BRAMBLE BIOMASS

^{P.223-231}
 (Figures 82-86)

356 The absolute weights of minerals found in each component were
 obtained by multiplying the dry weight of each component by the
 concentrations in Figures ^{P.212-15} 76-80. These combined concentrations were used
 rather than those of the individual areas, because the variability of the
 individual area curves obscured many of the underlying trends. However,
 because there were consistent differences between areas in mineral
 concentrations, use of the same set of concentration values for all three
 areas exaggerated some differences in absolute mineral weights. Other
 differences were under estimated.

357 For nitrogen where A had lower concentrations than B or C, the
 differences in total uptake between A and the others were too high. For
 calcium, where A had the higher concentrations, the differences were too
 low. Even for nitrogen, however, the greater dry weights found in A
 were sufficient to off-set the higher concentrations of nitrogen found
 in B and C. Thus total uptake for all five elements was greatest in A,
 least in C.

BIO MASS MAGNESIUM CONTENT-AREA A FIG 82



For Figs. 82-86 solid lines indicate total content of a particular element in each year's cane system, and the areas marked by letters show the contribution of the individual components to this total content.

FIG 82 cont

BIOMASS MAGNESIUM CONTENT

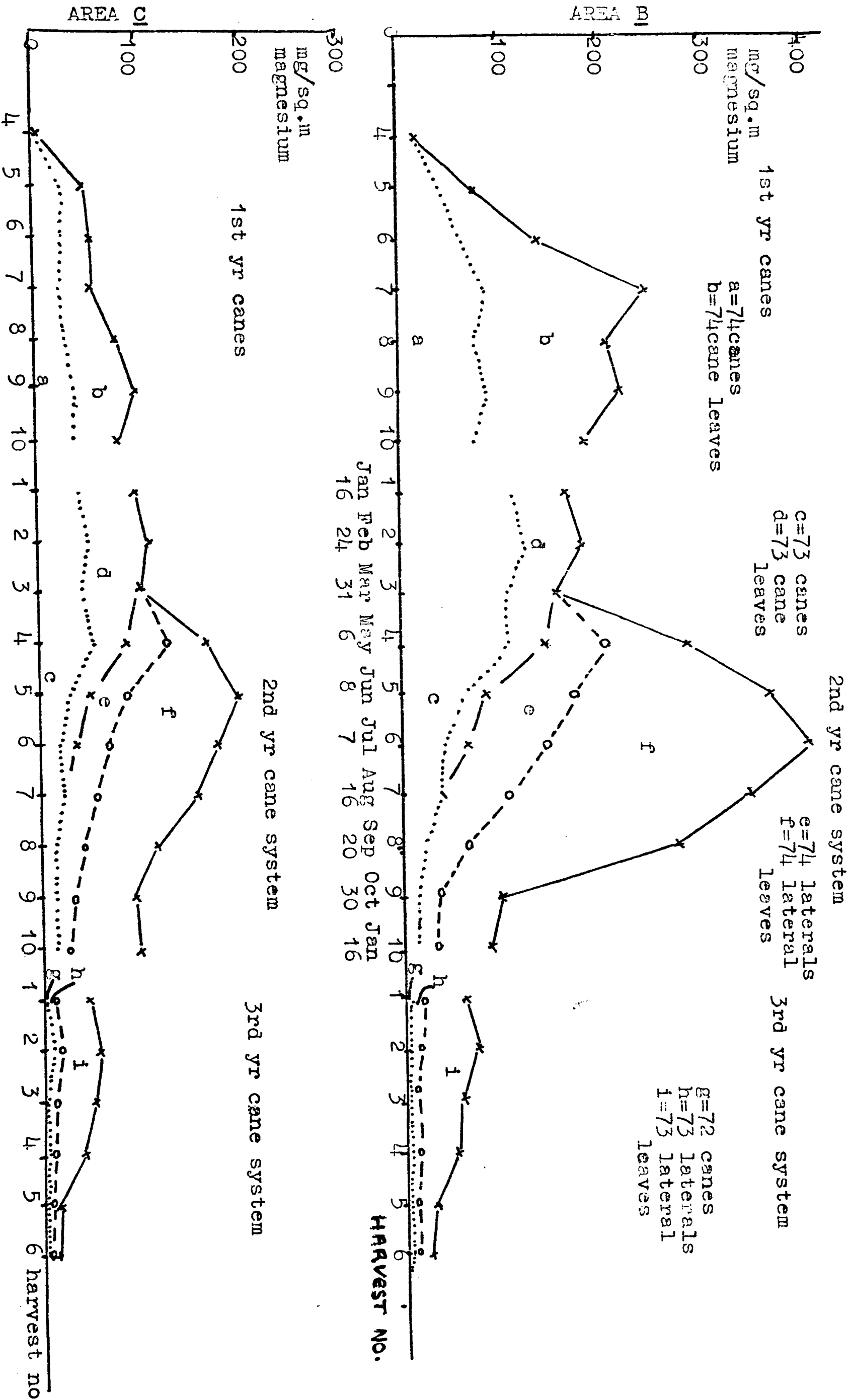
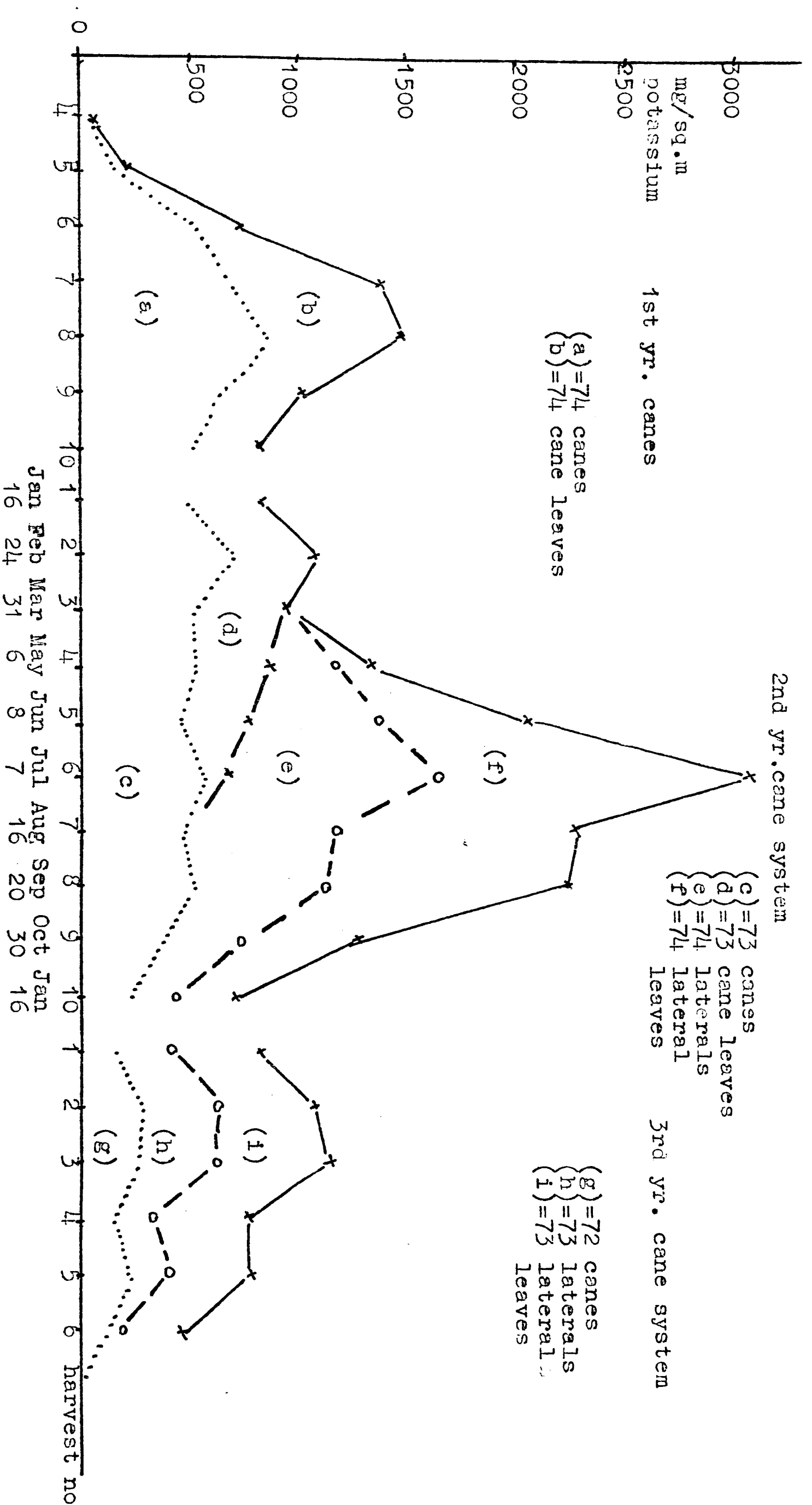


FIG 83.

BIOMASS POTASSIUM CONTENT-AREA A





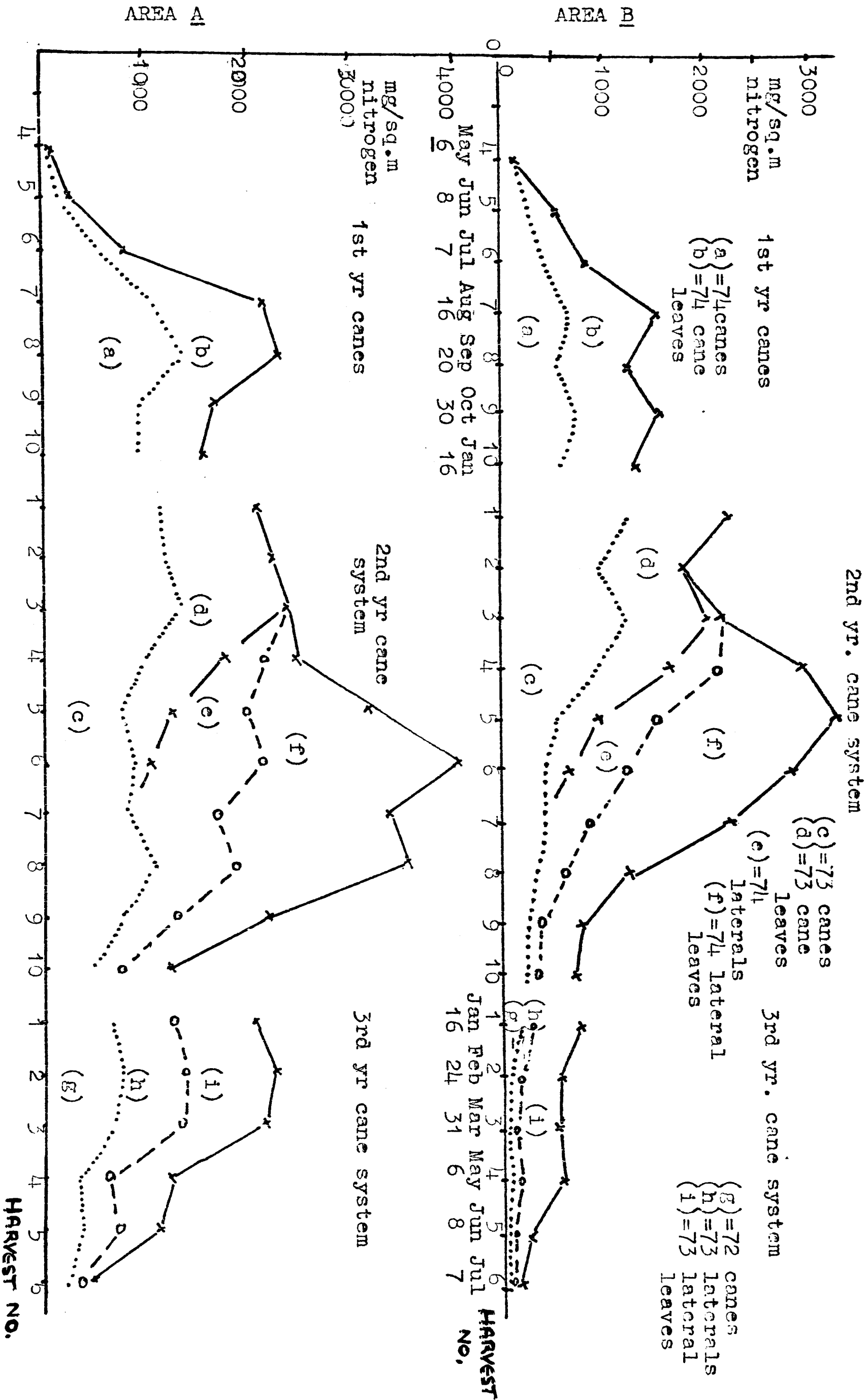
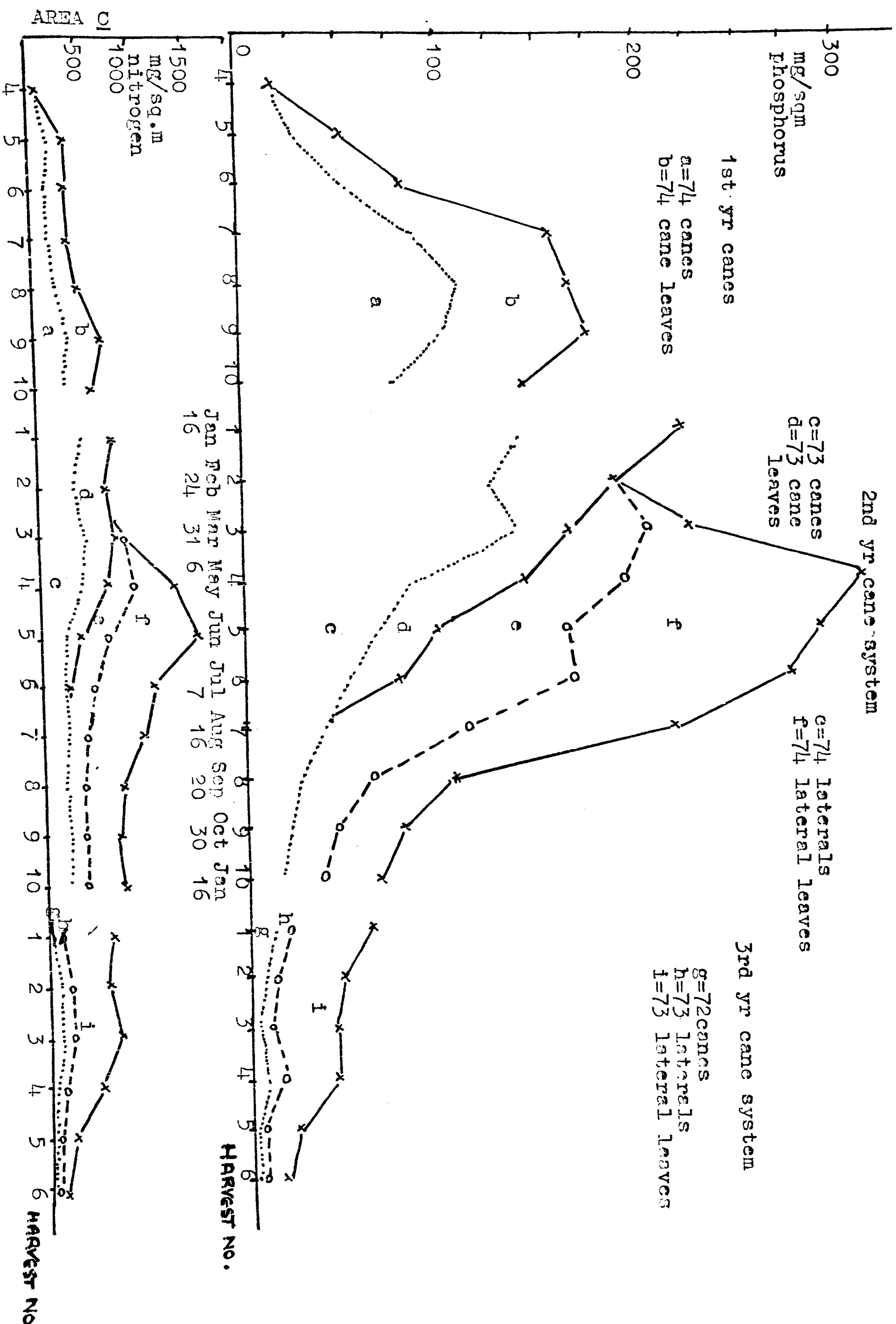


FIG 85

BIOMASS PHOSPHORUS CONTENT-AREA B

FIG 84 cont.
NITROGEN CONTENT



BIOMASS PHOSPHORUS CONTENT - AREA A

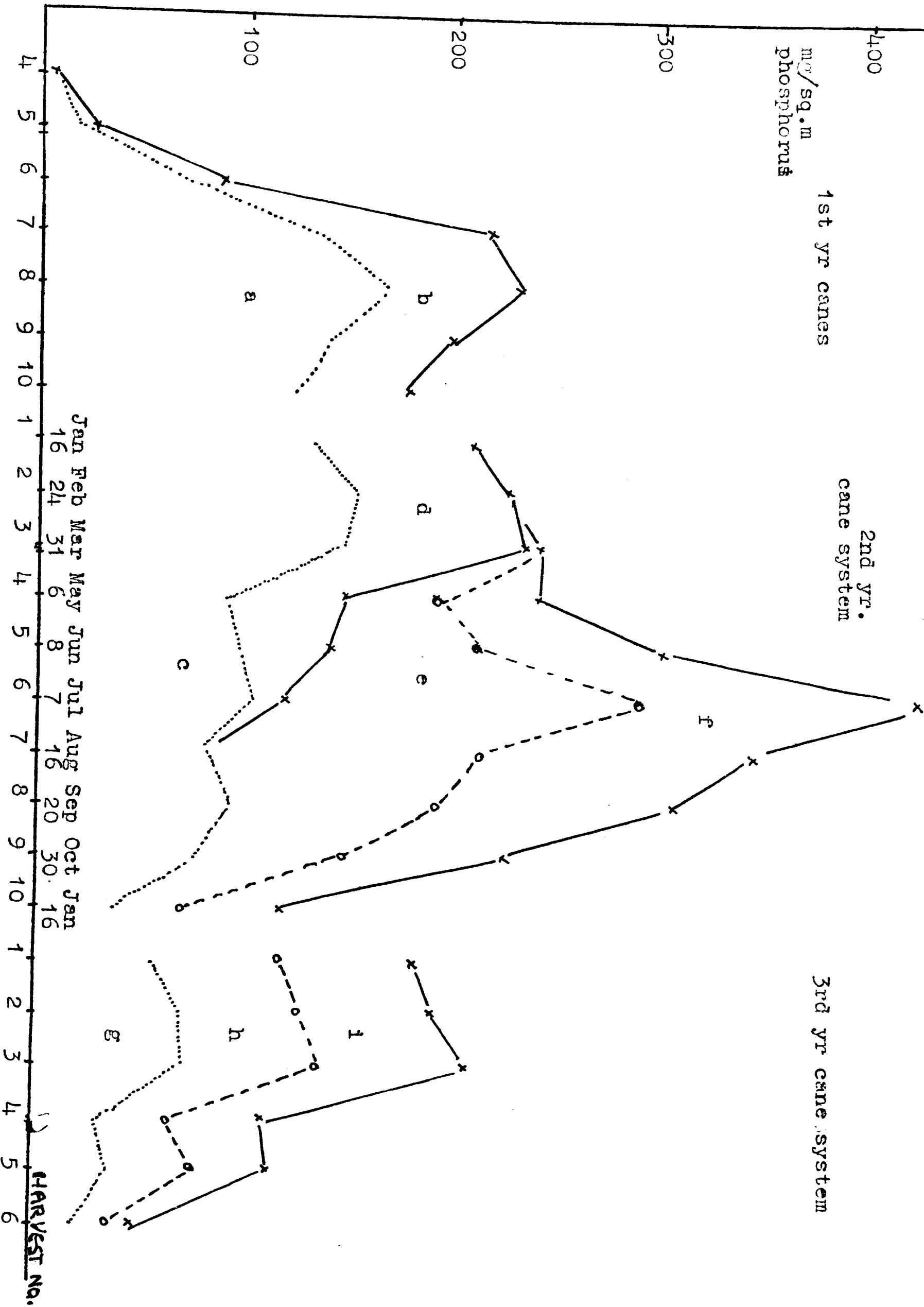


FIG 86
BIOMASS CALCIUM CONTENT

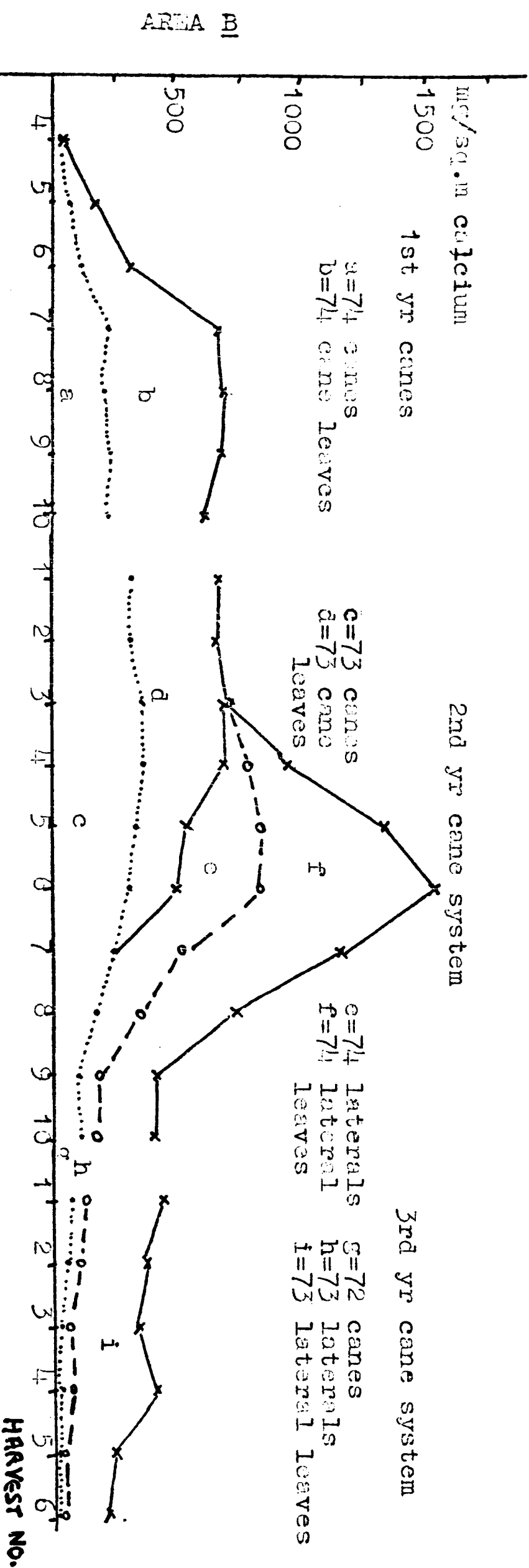
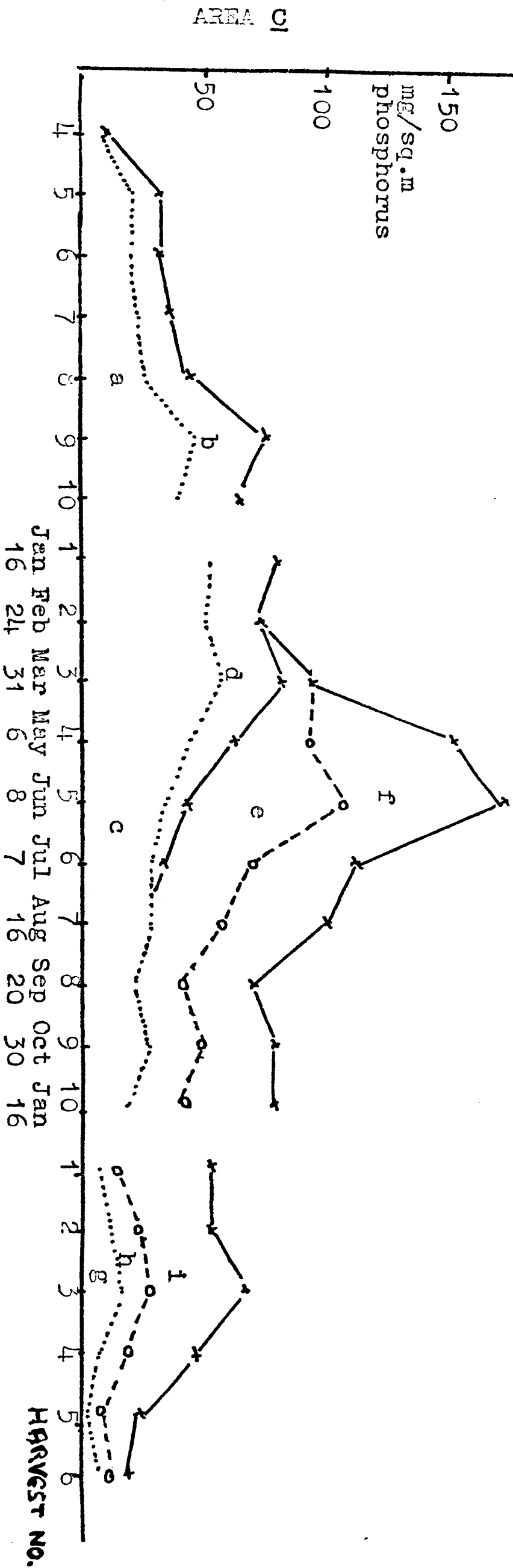


FIG 85cont.
BIOMASS PHOSPHORUS CONTENT



DISTRIBUTION OF MINERALS

358 **TOTAL ABOVE-GROUND WEIGHTS** The total amounts of minerals in the above-ground bramble showed a summer peak like the biomass^{P.221} (Table 62). The values found were in the same general range reported by Ovington (1956) for total undergrowth under different tree species. The changes in the total amounts in each cane system and the distribution of minerals between components are shown in Figures 82-86.^{P.223-231}

359 **FIRST-YEAR REQUIREMENT**^{P.233} Table 63 shows the maximum uptake into first-year canes for each area. It is not known how much of this was fresh uptake from the soil each year, how much from reserves of minerals withdrawn from dying canes into the rootstocks.

360 **SECOND-YEAR REQUIREMENT** During the second year there was considerable movement into the laterals and their leaves. Part of this came from storage in the canes and withdrawals from the dying cane leaves, part directly from the rootstocks.^{P.233} Also in Table 63 is the difference between the maximum content in the second-year cane system and the amount present at the beginning of the year. This gives the minimum that must have come from directly from the rootstock in the second year. In practice more uptake must have occurred as there was not 100% withdrawal from the cane leaves. The quantities required by first and second year cane systems were similar.

361 **STORAGE OF MINERALS IN FIRST-YEAR CANES** The concentration results indicated storage of nitrogen, phosphorus and magnesium in first-year canes. The quantities that were lost from the canes during lateral growth are shown in Table 64,^{P.234} along with the maximum requirements of the laterals and their leaves. Only 15-30% of this requirement was

TABLE 63 MINERAL UPTAKE BY FIRST AND SECOND YEAR
CANE SYSTEMS

Element	Area	1st yr. uptake	2nd yr. uptake (maximum content - content at H.1)	
Mg	A	355	407	mg/sq.m
	B	250	241	"
	C	98	99	"
Ca	A	1140	1551	"
	B	696	857	"
	C	285	412	"
N	A	2300	1953	"
	B	1585	1068	"
	C	664	833	"
P	A	231	221	"
	B	182	92	"
	C	73	98	"
K	A	1464	2237	"
	B	1033	1281	"
	C	398	692	"

TABLE 64

TRANSFER OF MINERALS FROM
2nd YR. CANES TO LATERALS

Element	Area	Estimate of minerals stored in cane. (mg/sq.m)			Maximum content of laterals and lateral leaves. (mg/sq.m)		
		A	B	C	A	B	C
P		56	74	30	311	201	97
Mg		70	82	33	489	346	146
N		567	659	363	3020	2373	1198

TABLE 65

MINERAL CONTENT OF STANDING DEAD AS
% NET TOTAL UPTAKE

Element	Area	A	B	C
K		7.0	2.6	2.3
Mg		17.7	6.0	8.8
P		21.8	7.9	7.5
N		35.0	12.1	12.5
Ca		45.0	16.9	23.2

TABLE 66 % TOTAL UPTAKE BY 1st YR. CANES OCCURRING
AFTER MAXIMUM MINERAL CONTENT IN
THE 2ND YR. CANE-SYSTEM

Element	Area	A	B	C
K		50	57	27
Mg		64	45	51
P		63	71	51
N		65	69	49
Ca		75	74	63

supplied from the stored minerals. The weight of the buds was about 0.1 - 0.2 g/cane or at most about 1000 mg per sq.m. It was thus clearly impossible for all of the stored minerals to be in the buds.

362 IMMOBILISATION OF MINERALS IN STANDING DEAD Not all of the minerals in the standing dead were withdrawn. Much entered the standing dead. ^{P.234} Table 65 compares amounts in the standing dead with the combined first and second-year requirement in a season. With the exception of the nitrogen and calcium figures in A, the standing dead mineral content was less than 25% of the season's uptake. Since the turnover time for the standing dead was only about 1-2 years, this component did not represent a serious immobilisation of minerals. There was, however, no information on how quickly nutrients were released once the standing dead was incorporated into the litter layer.

363 COMPETITION BETWEEN CANES OF DIFFERENT AGES The similarity of the first and second-year requirements for minerals suggests that canes on the same rootstock but of different ages might compete for minerals. This competition was reduced, however, by the differences in the timing of growth by laterals and by first-year canes. Much of the uptake into new canes took place after the end of lateral growth. ^{P.234} Table 66). This resembles the separation found in the development of leaves on canes and laterals. By spreading the growing season for the plant as a whole the difference in the timing of growth for the two types of stems allows a more effective exploitation of the environment.

STARCH CONTENT OF BRAMBLE STEMS

364 Starch analysis was carried out on the same material used in the mineral analysis. Various experiments had shown the dependence of lateral growth on cane reserves and storage of minerals in canes was demonstrated. Amor (1975) had reported that considerable quantities of starch were stored in the pith and medullary rays of canes.

365 METHOD The starch was extracted from the dried material using the method described in Allen (1974) involving boiling water extraction and the iodine-starch complex formation. Because there are diurnal variations in the starch content of leaves only stem material was analysed. It was hoped that long term trends in the stems would over-ride any daily variation.

RESULTS P. 237, 238.
Figures 87 and 88.

366 FIRST-YEAR CANES The rise in starch content and concentration occurred only after growth had ended and maximum leaf canopy formed. This fits with the results of the defoliation experiments which indicated that most of the reserves used for lateral growth were laid down in the autumn or winter. Carbohydrate exported from the more mature leaves on the canes prior to growth ending was probably used directly for further growth.

367 SECOND-YEAR CANES There was a rapid rise in starch concentrations and total starch content in second-year canes in the spring, which reached its peak as lateral growth began and the new canopy started to form. The probable cause of the rise was photosynthesis by the cane leaves as soon as conditions became favourable in spring. The starch formed was probably subsequently converted to sugars to supply

STEMS

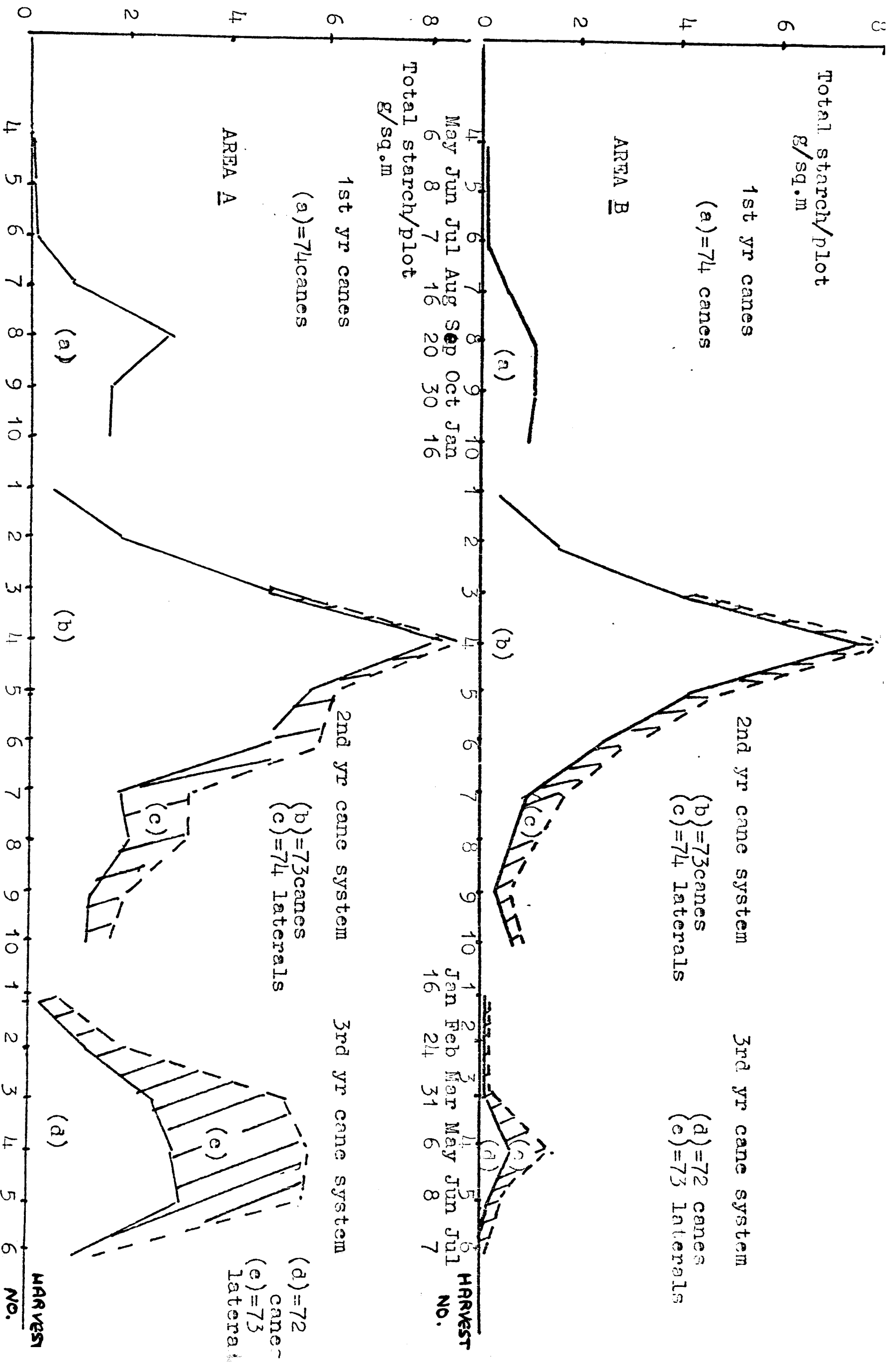


FIG 88

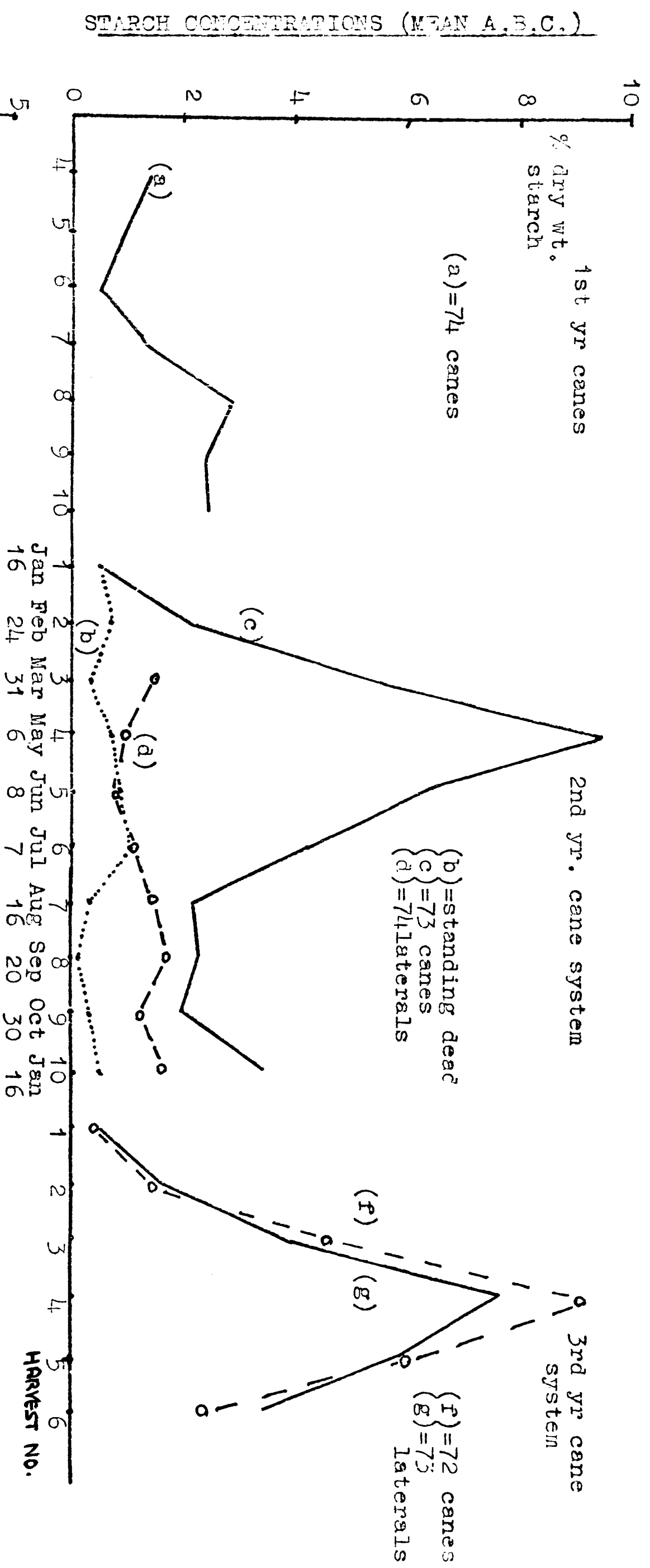
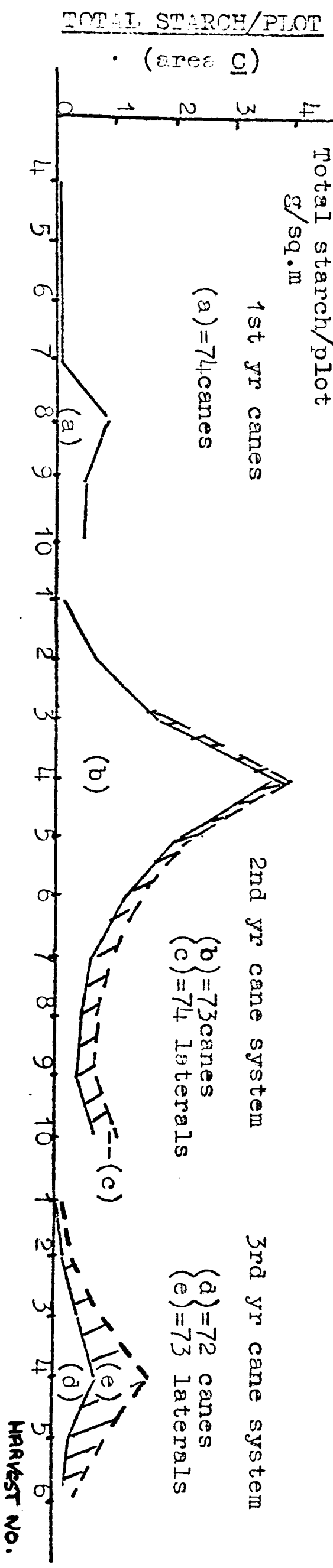


FIG 87



lateral growth. As with first-year cane growth there was no rise in the starch content during growth of the laterals.

368 **THIRD-YEAR CANE SYSTEM** Photosynthesis by the lateral leaves, which had over-wintered caused a rise in the starch concentrations and total amounts of both canes and laterals. This was similar to the rise in starch in the second-year canes. Concentrations of starch fell again as death of the 73 leaves occurred and much of the starch may have been converted to more mobile forms and transferred to the rootstocks.

369 **CONCLUSIONS** Storage of minerals in the first-year canes took place during growth of the cane. The build up of starch reserves however, took place largely in the early spring immediately before lateral growth. These measurements strengthen the view that the major advantage of the partial evergreen habit for bramble is the high photosynthetic capability which it provides for the beginning of the year before the new canopy has had a chance to establish.

CONCLUSIONS

SURVIVAL AND GROWTH OF BRAMBLE IN WOODLAND

370. The results from the survey by Field and Dawkins (In prepn.) showed the abundance of bramble in Wytham, with about 35% of the wood totally covered by bramble. A striking feature of the bramble cover was the sudden changes that occurred in the vigour and density of growth. These changes were shown to be related in many cases to differences in the nature of the overstorey. The contrast between growth under ash and under sycamore, two of the commonest trees in Wytham was particularly marked and also the effect of a shrub layer on growth below ash.

371. Periodic changes in the overstorey occur in all woods, whether natural, or, far more commonly in Britain, the results of thinnings, fellings and plantings by man. Part of the reason for the abundance of bramble is its ability to survive for long periods under deep shade and to show a rapid response to any local increase in the favourableness of the conditions. This was clearly demonstrated by the increases in growth that were found under quite small gaps. The relatively short life of the canes means that changes in growth can occur fairly rapidly.

372. When summer conditions are unfavourable, e.g. under a young beech canopy, some growth of laterals and first-year canes may still be possible because of reserves in second-year canes and rootstocks. Photosynthesis is possible in late autumn and spring, when the leaves are off the trees, because of brambles partial evergreen habit. Reserves laid down in this period can then be used for subsequent growth, the bulk of which occurs

while the tree canopy is present. Faster die-out of bramble under a developing pine stand would thus be expected than under even a dense-canopied deciduous species such as beech.

373. Vegetative reproduction, which is more common among less vigorously growing canes, is more effective at replacing dead rootstocks under marginal growth conditions than floral reproduction. The daughter plant has a much greater food base, in the parent cane, than the seedling. The chances of survival of the daughter plant are thus higher.

COMPARISON OF A BRAMBLE STAND WITH HERB AND SHRUB LAYERS

374. Bramble stands have similarities both with the herb and with the shrub layers in woodland. A dense thicket may be 1-2m high with a canopy held above the level of most herbs, while at other sites the canes sprawl amongst the herbs. There is a wide range of growth shown by bramble communities as was shown in Table 17, ^{P. 62} all of whose sites were dominated by Rubus fruticosus. The range of growth is shown in the size of plant as well as in the growth per unit area.

375. Estimates of annual, dry-weight turnover by the bramble shoot system are complicated by differences in the timing of growth between different ages of cane and by the uncertainties regarding transfers of materials between roots, canes and laterals. The estimates for Wytham are comparable to those reported for herb and shrub layers in other work, though below those for open-grown herb communities in Britain. Bramble stands larger than those measured in Wytham have been seen, so that open-grown bramble in Britain is probably comparable in annual dry-weight turnover to many grassland and other herb communities.

376. Unlike shrubs the top growth of bramble is not long lived. Most

of the stems live only 2 - 3 years, with another 1 - 2 years as standing dead before incorporation into the litter. The bulk of the biomass is in the second-year, flowering cane system. Thus the rate of turnover of dry matter although slower than for herbs is much faster than for shrubs where much is stored in the stems. This also applies to the major mineral elements, so that cycling of nutrients is fairly rapid.

377. Leaf-cover in a dense bramble stand is almost continuous. In a tree or shrub a continuous canopy is usually formed by branches off a main stem with the canopy of each individual plant more or less discrete. In a sprawling plant, such as bramble, complete cover is only formed by the interlacing of stems of different ages and from different plants. This results in the type of structure described on pages 124-6.

378. The structure of a bramble stand is an important characteristic. It determines the height of the bramble canopy and raises it above most woodland herbs. The effective leaf cover in summer is high because the leaves are mostly close to the horizontal. Since partial cover persists over winter, the light reaching the forest floor is reduced even at times when the leaves are off the tree canopy. The opportunities for other species, even those growing mainly in autumn or early spring, are thus considerably reduced.

379. The structure of a bramble stand also helps make it a weed. Movement through a bramble stand is difficult even after the top growth has been killed by sprays. The bramble thicket provides shelter for undesirable species, whether these are rabbits, or trees on a common being encroached by scrub. The build up of standing dead, which is very dry and brittle, in the lower parts of the stand may constitute a fire hazard in hot weather.

DISTRIBUTION AND MOVEMENT OF NUTRIENTS IN THE PLANT

380. The growth of the different stem components is partially based on reserves already present and part on photosynthesis by the leaves of the growing stem. Stem photosynthesis appeared to be small. Most of the growth by first-year canes could be supported by rootstock reserves. During growth by the first-year canes there was storage of nitrogen, phosphorus and magnesium, and a build up of starch in the canes after growth ended. Further starch was laid down in the early spring as a result of the activity of leaves that remained over winter.

381. As with cane growth, lateral growth could be partially supported by reserves, in the second-year canes. There was a transfer of stored minerals to the laterals and a decline in the levels of cane starch during the laterals' growth.

382. During die-back of canes and laterals in the autumn and spring material was withdrawn from the dying tissues. This was indicated by the falls in concentrations of the major mineral elements (except calcium) and the fall in the levels of starch in old stems after an initial spring rise. Some of the products of photosynthesis by leaves on first-year canes in the autumn may also be returned to the rootstocks, as well as appearing as starch in the canes. When bramble topgrowth was cleared in the autumn any such returns to the rootstocks were prevented and subsequent stem growth was reduced.

383. Potential for competition existed between growth of first-year canes and that of laterals on second-year canes on the same rootstock. Both contributed about equally to the annual dry-weight turnover of the stand. The net uptake of minerals into first and second-year canes was similar. Both types of stem bore leaves which could compete for space in the bramble

canopy. There was, however, no evidence for negative interactions between the two types of growth.

384. The timing of the main periods of growth for canes and laterals were quite distinct. The main lateral growth occurred about six weeks earlier than the main period of cane growth, in Wytham. Lateral leaves formed the bulk of the pre-flowering canopy, but cane leaves became important in the autumn and over winter, as most of the lateral leaves were lost after fruiting. Nearly 60% of cane mineral uptake occurred after ^{extension} of laterals had ended. This staggering of the main periods of growth, nutrient demand, and leaf cover between the two types of stems, allows for a more effective use of environmental resources, as well as giving more scope for internal nutrient cycling.

REPRODUCTION BY BRAMBLE

385. The two forms of reproduction, vegetative and floral, appeared to be complementary in the areas studied. This was partly brought about by the opposite relations between vigour of growth and flowering, and vigour of growth and tip-rooting. Growth of laterals and flowering increased in areas of vigorous cane growth because of greater cane reserves. Vegetative reproduction was reduced, however, because such canes showed a lesser tendency to tip-root. The dense structure, characteristic of high vigour areas, also reduced the chances of tip-rooting occurring because there was more support for the canes.

386. This type of interaction is ecologically advantageous. In a high density, high vigour stand, increase in seed production favours spread over long distances to new sites. In a low density or low vigour stand, where intra-specific competition is low, vegetative reproduction is more

effective in allowing a thicket to spread, particularly where conditions are unfavourable. This is because of the higher reserves of the daughter plant compared to the seedling.

389. The daughter plant in some ways resembles a lateral in that it depends for its survival and growth on reserves in the parent cane. Transfer to the new plant starts as soon as rooting has occurred and continues through the winter, spring and early summer. Most of the material for the growth of the new plant can be supplied from the section of cane nearest the daughter plant.

388. The new cane on the daughter plant is a more effective sink for the parent cane resources than a lateral; its growth is more than laterals in an equivalent position on the parent cane. Some competition for nutrient occurs between laterals and the daughter cane, treatments affecting one may alter growth of the other. There is, however, only one daughter cane to several laterals on the parent cane. Also the section of parent cane which can supply the bulk of the new canes requirements, i.e. the terminal section of the parent cane, frequently bears few laterals. Thus the amount of competition between the laterals and the daughter cane is only small.

389. Transfers between parent cane and daughter plant are not necessarily all one way. If the parent cane is separated from its root-stock, the daughter roots can supply most of the requirements for survival and lateral growth by that cane. Thus the normal directions of flow in the conducting tissues are reversed.

390. The unusual growth pattern of bramble and its abundance in woods such as Wytham are sufficient justification perhaps for a study of this nature. In addition certain aspects may be relevant to the problem of bramble as a weed and means of its control. There is considerable scope for further work particularly in the fields of movement of material between different parts of the plant and the mechanisms by which tree competition affects bramble growth. There is also the whole range of possible differences between the species comprising the bramble aggregate, which may limit the applicability of these results to other sites.

SUMMARY OF RESULTS

BRAMBLE BIOMASS AND ANNUAL TURNOVER OF DRY WEIGHT

On three sites studied in Wytham, total bramble biomass was found to vary from 90 - 263 g/sq.m in winter, and from 149 - 438 g/sq.m in summer. Other workers have recorded summer biomass values of 34 - 83 g/sq.m for bramble in woodland in Britain. In Australia species introduced from Britain have given biomass values of 850 g/sq.m and 1850 g/sq.m when growing in the open. Thus while the Wytham sites are clearly highly productive for bramble in woodland in Britain, they are well below the potential limits of bramble growth.

Annual turnover of bramble dry-weight in Wytham was estimated as being from 60 - 300 g/sq.m/year (0.6 - 3 tonnes/ha/yr). This is similar to other reports for herb and shrub layers in woodland, but is low compared to open grown herb communities in Britain of 400 - 1300 g/sq.m/yr. (4 - 13 tonnes/ha/yr).

RESPONSE OF BRAMBLE TO OVERSTOREY

In the year following creation of a gap in the tree canopy, the bramble immediately beneath the gap was estimated to have increased from 192 g/sq.m to 323 g/sq.m (winter biomass). In the second year of growth after the gap was made, summer biomass was 428 g/sq.m compared to 281 g/sq.m in the control plots. Under "older" gaps the growth was found to be up to six times that in the surrounding shade.

Large variations in bramble growth were shown to be associated with differences in the tree species forming the overstorey. Mean

percentage cover of bramble in plots under ash, oak and sycamore were 61, 50 and 16% respectively. The presence of a shrub understorey was found to reduce mean bramble cover beneath ash, progressively as the shrub cover increased. Under sycamore, however, the level of bramble growth was unaffected by the presence of the additional shrub canopy.

NON DESTRUCTIVE METHODS OF PLOT MEASUREMENT

Simple point quadrats, consisting of a pin lowered vertically from a frame, were found to be useful for estimating the quantity and distribution of leaves in a bramble canopy. An r^2 of 0.78 was obtained for a regression of total leaf area per plot on number of leaf hits for leaves during the summer. The correlation between the two decreased over winter because leaf angles increased. Point quadrats were not found to be of any use in estimating quantities of bramble stem present and hence total plot dry weight.

A regression was calculated of stem length per plot on Intersection Value - the number of apparent intersections between stems in the plots and lines across it. This had an r^2 of 0.73. The relation became weaker in the taller bramble plots because the greater the angle of stems to the horizontal the smaller their effective horizontal length, which is what intersection sampling estimates.

Multiplying the Intersection Value of a plot by its mean canopy height gave a figure which proved useful for estimating the dry weight of plots without the need for destructive sampling. The relation was stable over the year and was applicable to bramble stands up to about 600 g/sq.m.

ANATOMY OF A BRAMBLE STAND

Three layers were distinguished in the high density bramble stands

found in Wytham. The uppermost of these contained the bulk of the leaves. The interlacing of stems was found to increase the height of a vigorous bramble stand raising the canopy above most other woodland herbs. Below this is a layer mainly consisting of second year canes and the remains of the previous years' canopy. The bottom zone contains most of the standing dead.

COMPARISON OF FIRST AND SECOND YEAR GROWTH

The main periods of growth for laterals and for first-year canes were found to be staggered, cane growth being about six weeks later than laterals. This had been found for less vigorous stands of bramble by Sykes and Taylor (In prepn.).

Competition between canes of different ages on the same root-stock was reduced by this difference in the timing of growth. About 60% mineral uptake into first year canes was found to occur after the maximum mineral content had been reached in second year canes. Cane leaves were shown to form the bulk of the autumn and winter canopies whereas lateral leaves contributed more to the summer canopy.

TRANSFER OF MATERIALS BETWEEN ROOTS, CANES AND LATERALS

Defoliation experiments showed that transfer of material from roots to first year canes could support up to 80% of normal cane growth. Similarly about 50% of lateral growth appeared to be based on reserves in the canes. Build up of starch in the autumn, late winter and early spring was detected in the canes. This starch disappeared during lateral growth. This suggests that photosynthesis by overwintering leaves was important. Nitrogen phosphorus and magnesium were found to be stored in first-year

canes and transferred to the laterals during their growth.

REPRODUCTION

In the areas studied, vegetative and floral reproduction were found to be complementary as for R. caesius (Abrahamson 1975). Vegetative reproduction was greatest in areas of low vigour as expected from the work of Barnola (1971) on individual canes, though in the field low vigour was confounded with poor stand structure which meant that cane tips were more likely to contact the ground. Flowering success was shown to be related to growth vigour through the correlation with lateral length. It is thought that vigour of growth may provide a mechanism whereby the relative levels of the two forms of reproduction are controlled.

Daughter plants were found to depend on the parent cane for their early growth, not the parent rootstock, and particularly the metre of cane nearest the daughter. Transfers to the daughter plant were shown to take place from November till July. If the daughter was separated from the parent cane, its future survival and growth were ^{found} to depend on the length of time since the cane originally rooted and the length of the parent cane left attached to the daughter. The daughter rootstock was found to be able to support the parent cane if that were separated from its rootstock. Lateral growth on such a cane was only slightly affected.

These results are the first quantitative study of bramble on a highly productive (for bramble) woodland site and confirm many of the findings about the growth pattern for less productive woodlands. The results provide information on the partitioning of material within the plant and demonstrate the marked response by bramble to different intensities of tree overstorey competition.

REFERENCES

- Abrahamson W.G. (1975) Reproductive Strategy in dewberries. Ecology 56: 721-26.
- Adamson R.S. (1932) Notes on the natural regeneration of woodland in Essex. J. Ecol. 20: 152-56.
- Allen D.E. (1971) in "Hedges and Local History". National Council of Social Service, London.
- Allen S.E. (ed) (1974) "Chemical Analysis of Ecological Materials" Blackwell Scientific Publications, Oxford.
- Amor R.L. (1971) "A Study of the Ecology and Control of Blackberry (Rubus fruticosus L.agg)" Ph.d thesis, Monash University, Victoria, Australia.
- Amor R.L. Ecology and Control of Blackberry (Rubus fruticosus L.agg)
- (1973) (1) Rubus spp. as weeds in Victoria. Weed Res. 13: 218-23.
- (1974a) (11) Reproduction. Weed Res. 14: 231-38.
- (1974b) (111) Response of R. procerus to mechanical removal of top growth to foliar applied herbicides. Weed Res. 14: 239-43.
- (1975) (IV) Control by pichloram granules. Weed Res. 15: 47-52.
- Anderson R.C., Loucks O.L. and Swain A.M. (1969) Herbaceous response to canopy cover, light intensity and throughfall precipitation in coniferous forests. Ecology 50: 255-63.
- Barnola P. (1971) Recherches sur le déterminisme du marcottage de l'extrémité apicale des tiges de la ronce, R. fruticosus L.agg. Rev. Gén. Bot. 78: 185-99.
- Beijerinck W.,^{and} ter Pelkwyk A.J. (1952) Rubi in the north-eastern part of the Netherlands. Act. Bot. Neer. 1: 325-60.
- Beijerinck W., (1953) On the habit ecology and taxonomy of the brambles in the Netherlands. Act. Bot. Neer. 1: 523-45.
- Brown R.M. (1975) "Chemical Control of weeds in forests". Forestry Commission Booklet 40: H.M.S.O. London.
- Buffon G. (1777) Essai d'arithmétique morale. Supplement à l'Histoire Naturelle 14.

- Bunce R.G.H. (1968) Biomass and production of trees in a mixed deciduous woodland (1) Girth and height as parameters for the estimation of tree dry weight. *J. Ecol.* 56: 759-75.
- Chapman N. and D. (1975) "Fallow Deer" Terence Dalton Ltd., Lavenham, Suffolk.
- Clapham A.R., Tutin T.G. and Warburg E.F. (1962) "Flora of the British Isles" 2nd Ed. Cambridge University Press.
- Conard H.S. (1951) "The background of plant ecology" Iowa State College Press, Ames, Iowa, U.S.A.
- Crandall P.C. Chamberlain J.D. and Biderbost K.A. (1974a) Cane characteristics associated with berry number in red raspberry. *J. Amer. Soc. Hort. Sci.* 99: 370-72.
- ditto (1974b) Influence of cane number and diameter, irrigation and carbohydrate reserves on the fruit number of red raspberries. *J. Amer. Soc. Hort. Sci.* 99: 524-27.
- Duvigneaux P. and Denacayer-De Smet S., (1967) in "Symposium on primary productivity and mineral cycling in natural ecosystems" Young H.E. (ed.) Orono University Maine Press. 1968.
- Ford E.D. and Newbould P.J. (1971) The leaf canopy of a coppiced deciduous woodland. (1) Development and Structure. *J. Ecol.* 59: 843-62.
- Gimingham C.H. (1972) "Ecology of Heathlands" Chapman and Hall U.K.
- Gorham, E. and Pearsall W.H. (1956) Production Ecology (1) Standing crops of natural vegetation. *Oikos* 7: 193-201.
- Grayson A.J. and Jones E.W. (1956) "Notes on the history of Wytham Estate with particular reference to the woodlands". Imperial Forestry Institute, Oxford.
- Grieg-Smith P. (1964) "Quantitative Plant Ecology" 2nd Ed. Butterworths. London.
- Heslop-Harrison Y. (1959) Natural and induced rooting of the stem apex in Rubus. *Ann. Bot. N.S.* 23: 307-18.
- Hughes M.K. (1971) Ground vegetation biocontent and net production in a deciduous woodland. *Oecologia* 7: 127-35.
- Jackson M.L. (1958) "Soil Chemical Analysis" Prentice-Hall.

- Kestemont P. (1971) Biomasse et productivité aériennes d'un tallis de chères et bouleaux riche en ronces au plateau de Robiet (Vresse) Bull. Roy. Bot. Soc. Belg. 104: 104-13.
- Lees E. (1884) *Remarks on the mode of growth of the British Rubi.* Trans. Bot. Soc. Edinburgh 1: 172-78.
- Loetsch F, Zohro F. and Haller K.E. (1973) "Forest Inventory Vol. 2" B.L.V., Verlagsgesellschaft, Munchen.
- Madgwick H.A.I. (1965) Weights and nutrient composition of understorey species in an ashwood. J. Ecol. 53: 335-41.
- Newman E.I. (1966) A method of estimating the total length of root in a sample. J. App. Ecol. 3: 139-45.
- Northcroft E.F. (1927) The blackberry pest. (1) Biology of the plant. N.Z.J. Agric. 34: 376-88.
- Novozamsky I., van Eck R., van Schouwenburg J. and Walinga I. (1974) Total nitrogen determination in plant material by means of the indophenol-blue method. Neth. J. Agric. Sci. 22: 3-5.
- Oredsson A. (1975) Factors possibly influencing the range of shrubby Rubus species in Sweden. (1) Severity of winter. Botaniska Notiser 128: 47-54.
- Ovington J.D. (1955) (1110) Studies of the development of woodland conditions under different trees. The ground flora. J. Ecol. 43: 1-21. (1956) (v) The mineral composition of the ground flora. J. Ecol. 44: 597-604.
- Robertson M. (1957) Further investigations of flower bud development in the genus Rubus. J. Hort. Sci. 32: 265-73.
- Rudolff C.F., Lenz F. (1960) The potential fertility of currant flowers. Eruerbsobstbau 2: 214-17 (Hort. Abst. 31: 2113).
- Salisbury E.J. (1918) The oak-hornbeam woods of Hertforshire. J. Ecol. 6: 14-47.
- Snedecor G.W. and Cochran W.G. (1967) "Statistical Methods". Iowa State University Press, Ames, Iowa.
- Sykes J.M. and Taylor K. (In press) from "The Ecology of Meathsp Woods" ed. J.E. Satchell. Springer-Verlag Berlin.

- Tamm C.O. (1950) Growth and plant nutrient concentration in Hylocomium proliferum (L) Lindb. in relation to tree canopy. Oikos 2: 60-64.
- Tansley A.G. (1949) "The British Isles and their Vegetation" Vol. 1. Cambridge University Press.
- Thrower S.L. (1962) Translocation of labelled assimilate in Soybean. (11) The pattern of translocation in intact and defoliated plants. Aust. J. Biol. Sci. 15: 629-59.
- Von Pein J.R. (1961) Blackberry controlled by goats and electric fence. N.Z.J. Agric. 103: 535.
- Williams I.H. (1960) (v) Effects of environment on Rubus idaeus L. Dormancy and flowering of the mature shoot. J. Hort. Sci. 35: 214-20.
- Winkworth R.E. (1955) The use of point quadrats for analysis of heathland. Aust. J. Bot. 3: 68-81.
- Warren Wilson J. (1960) Inclined point quadrats. New Phytologist 59: 1-8.
(1963) Errors resulting from the thickness of point quadrats. Aust. J. Bot. 11: 178-88.
- Watson W.C.R. (1958) "Handbook of the Rubi of Great Britain and Ireland" Cambridge University Press.
- Watt A.S.
(1924) The ecology of British beechwoods with special reference to their regeneration. The development and structure of beech communities on the South Downs. J. Ecol. 12: 145-204.
(1925) The development and structure of beech communities on the Sussex Downs. J. Ecol. 13: 27-73.
- Watt A.S. (1934) The vegetation of the Chiltern Hills with special reference to the beechwoods and their seral relationships. J. Ecol. 22: 445-507.
" (1947) Pattern and process in the plant community. J. Ecol. 35: 1-22.

APPENDIX I

METHOD USED FOR PHOSPHORUS DETERMINATION

This method is a modification of that in Jackson (1958) and was given to me by Dr. P.S. Lloyd.

Soln. A 0.5862 g Ammonium vanadate in 500ml water.

Soln. A* 20ml of the above made up to 500ml with water and 0.1ml concentrated nitric acid.

Soln. B 0.5 g Ammonium molybdate dissolved in 250ml of water plus 1.2ml conc. nitric acid in 150ml water, made up to 500ml.

Immediately before the test solutions A* and B are mixed.

TEST PROCEDURE 100mg of sample were ashed, the residue taken up in 1ml dilute nitric acid and made up to 10ml with water. 1ml of this was then made up to 10ml with water. A suitable aliquot was then added to 5ml of the A*, B mixture and this made up to 10ml. The colour was then allowed to develop for 15 minutes before reading it at 343 nm.

APPENDIX 2 STATISTICAL METHOD

Response curve analysis (Snedecor^{and COCHRAN} 1967) was used to test the significance of changes in dry weight over the season for each component. This method was suggested by Dr. Dawkins because it allows the testing of the significance of the shape of a curve, or section of a curve. Thus the peak in biomass area C, Fig. 7. p.34, was shown to be significant by this analysis, the trough in standing dead, Area A H.2-6, Fig. 8 p.34, to be non-significant at the $p = 95\%$ level. The method applies strictly only where the intervals between successive points are equal. Most of the harvest intervals were 4-6 wks and the use of the method was considered to be valid.